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Research Article

Invasive *Prunus serotina* and *Robinia pseudoacacia* impact on understory vegetation is species-, habitat-, and season-specific

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Abstract

Although the impact of invasive species on understory diversity has been extensively studied, most authors have compared invaded and non-invaded stands. Various authors have demonstrated different negative, positive, or no impacts of invasive trees on understory vegetation biodiversity. In our study, we aimed to assess the relationship between alpha diversity and species composition of the understory and the increasing aboveground biomass of two invasive trees, *Prunus serotina* and *Robinia pseudoacacia*. We assessed this relationship for two seasons (spring and summer) and two habitats (nutrient-rich habitats with oaks *Quercus petraea* and *Q. robur* and nutrient-poor habitats with Scots pine *Pinus sylvestris*) separately. We demonstrated a statistically significant relationship between understory species composition and increasing biomass of both invaders in both habitats in both seasons, except in nutrient-rich sites with *R. pseudoacacia*. In summer, we found indicator species for both invasive species in both habitats, while in spring, only for the nutrient-rich habitat with *P. serotina*. In nutrient-rich habitats, we did not find any significant effect of increasing *P. serotina* biomass on alpha diversity indices. In nutrient-poor habitats, *P. serotina* biomass was positively correlated with taxonomic and functional diversity but not significantly related to phylogenetic diversity. In summer, *R. pseudoacacia* biomass was positively correlated with taxonomic diversity in poor habitats and with functional dispersion but negatively correlated with mean pairwise phylogenetic distance. In nutrient-rich habitats, we observed a positive relationship between *R. pseudoacacia* biomass and phylogenetic diversity and a negative relationship with functional dispersion. Therefore, our results indicated high variability and context-dependence of invader impacts, related to invader species, understory species, habitat, and season. We confirmed that the relationship between invader biomass and nitrophilous, ruderal species is positive, while it is negative with forest specialists, especially on nutrient-poor sites.

Key words: Black cherry, black locust, functional diversity, indicator taxa, invasion ecology, phylogenetic diversity, seasonality, taxonomic diversity

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Introduction

Invasive species are one of the greatest threats to biodiversity (Richardson et al. 2000; Brondízio et al. 2019; Roy et al. 2024). Invasive trees as 'transformers' (*sensu* Richardson et al. 2000) can significantly change native ecosystems (Crooks 2002; Corenblit et al. 2014; Jagodziński et al. 2024). The changes in, e.g., nutrient cycling (Rice et al. 2004; Aerts et al. 2017) or light availability (Starfinger et al. 2003; Dyderski and Jagodziński 2019; García et al. 2023) can positively impact some

understory plant species, but some of them can retreat from transformed, invaded habitats (Chabrerie et al. 2008; Langmaier and Lapin 2020; Woziwoda et al. 2021; Bury and Dyderski 2025a, b).

In European forests, *Prunus serotina* Ehrh. (black cherry) and *R. pseudoacacia* L. (black locust) are among the most widespread non-native tree species (Wagner et al. 2017; Brus et al. 2019). *Prunus serotina* in Central European conditions is mostly a shrub or low tree (Starfinger et al. 2003; Bury and Dyderski 2024b, 2025a; Engel et al. 2024; Nyssen et al. 2024) and is mostly dispersed via zoochory and barochory (Starfinger et al. 2003; Deckers et al. 2008). This species does not have nitrogen-fixing abilities and is an early/mid-successional species mostly occurring in stand gaps (Godefroid et al. 2005; Closset-Kopp et al. 2007). *Robinia pseudoacacia* has different growing forms. It can be a shrub or a low or high tree (Bury and Dyderski 2025a). This pioneer species (Cierjacks et al. 2013; Vítková et al. 2017; Martin 2019) has nitrogen-fixing abilities (Rice et al. 2004; Vítková et al. 2017) and is mainly dispersed via barochory and anemochory (Vítková et al. 2017). Additionally, next to sexual, also vegetative reproduction by root suckers is an important way to settle in a new place (Cierjacks et al. 2013; Bouteiller et al. 2023) (Fig. 1a).

Vascular plants are the most studied taxonomic group in the case of the invasive trees effect on biodiversity (Vilà et al. 2024). Up to 2022, Wohlgemuth et al. (2022) identified 720 cases of different non-native trees effects on different vascular plant diversity attributes. Among them, 191 cases show non-significant relationships, 14 negative, and 21 positive effects of *P. serotina* on vascular plant diversity attributes. For *R. pseudoacacia*, 144 studies show non-significant relationships, 19 decreasing, and 31 increasing effects (Wohlgemuth et al. 2022). However, there is a noticeable difference in the study of the impact of both *P. serotina* and *R. pseudoacacia* at the species and community levels. According to the recent review by Vilà et al. (2024), there are only a few studies that focus on examining the impact of the abovementioned invasive tree species at the species level (Halarewicz and Pruchniewicz 2015). On the community level for *P. serotina*, among 90 studies about the impact on plants, 70 are about plant diversity; for *R. pseudoacacia*, among 46 studies, 32 are about plant diversity (Vilà et al. 2024). However, some previous studies revealed both negative and positive effects of studied invasive trees on individual species (e.g., Chabrerie et al. 2008; Halarewicz and Pruchniewicz 2015). There are important studies focused on *P. serotina* and *R. pseudoacacia* cover as quantitative indicators. Most of the studies about the impact of both *R. pseudoacacia* (Rahmonov 2009; Qiu et al. 2010; Benesperi et al. 2012; Trentanovi et al. 2013; Lazzaro et al. 2018; Sitzia et al. 2018; Gentili et al. 2019; Slabejová et al. 2019, 2023; Dyderski and Jagodziński 2021) and *P. serotina* (Verheyen et al. 2007; Halarewicz and Żołnierz 2014; Gentili et al. 2019; Dyderski and Jagodziński 2021) on understory plant diversity focused on comparing invaded and non-invaded stands. In contrast, only a few studies assessed the effects of invasive trees along their abundance gradient. Abundance gradient is important, as it not only reveals the thresholds of impact (Dickie et al. 2011) but also can be used as a space-for-time substitution in predicting the effects of invasive species spread (López-Núñez et al. 2017). There are only a few studies on *P. serotina* (Chabrerie et al. 2008, 2010; Bury and Dyderski 2024a) and *R. pseudoacacia* (Montecchiari et al. 2020) per capita effect on understory plants. For *P. serotina*, we showed a small positive relationship between the proportion of its biomass and species and functional richness. However, the study concerned a single forest complex, which is the Wielkopolska National Park, under

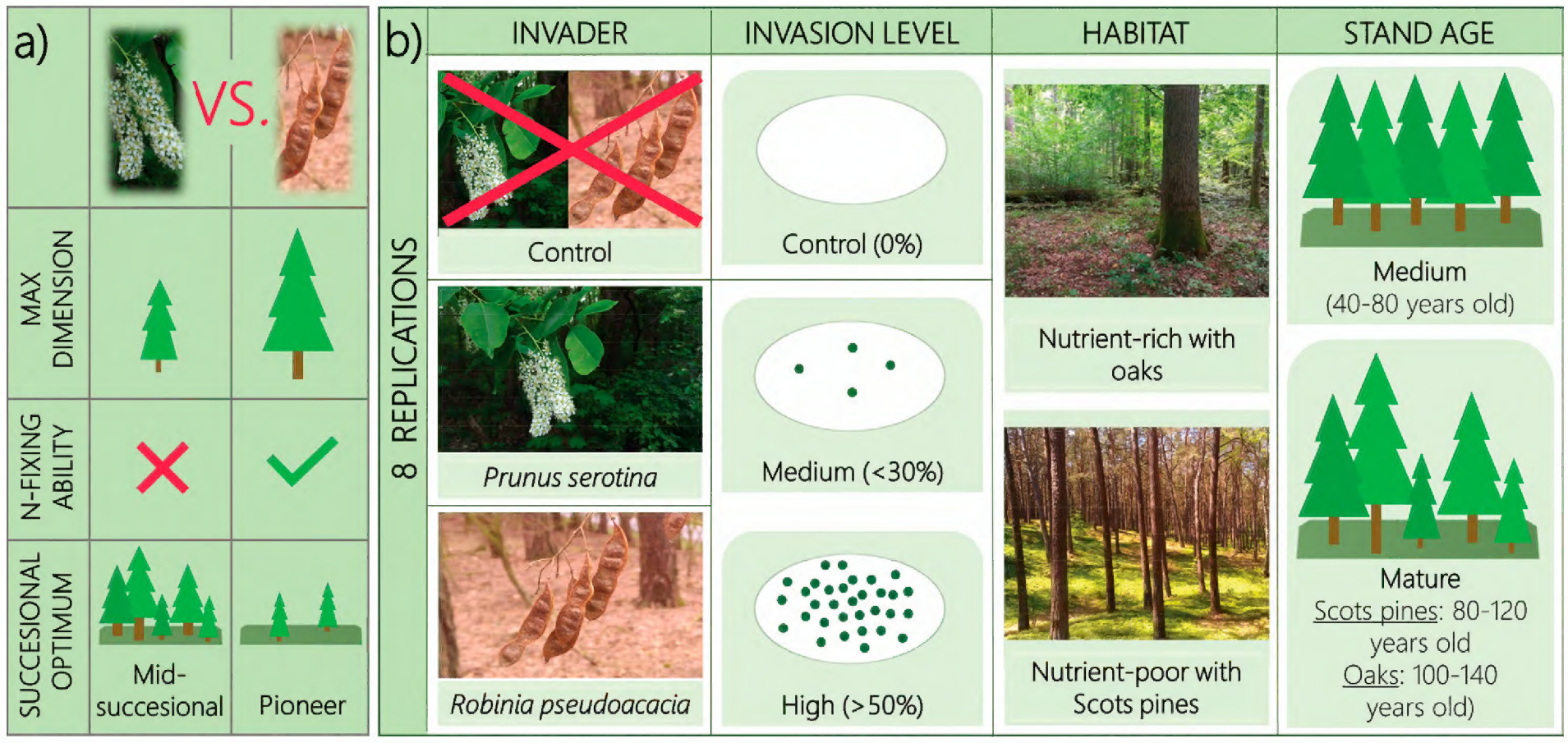

Figure 1. Comparison of studied invasive tree species (**a**) and study design (**b**).

a nature conservation regime. It is more difficult to apply the conclusions drawn from the cited work on a larger spatial scale, even within the same region. Previous studies revealed that abundance moderates the effects of *P. serotina* and *R. pseudo-acacia* on natural regeneration (Bury and Dyderski 2025a) and bryophytes (Bury and Dyderski 2025b). Studies on other invasive trees revealed negative (García et al. 2023) or non-linear (initial increase and subsequent decline in species richness) (Dickie et al. 2011) impact of invader biomass on understory diversity.

The vegetation of the understory is not the same throughout the entire growing season (Rautiainen et al. 2011). These differences are determined by phenology (Miller et al. 1997; Kudo et al. 2008), as many species have their peak flowering in spring, when the trees have not yet developed leaves (Heinrich 1976; Kudo et al. 2008; Heberling et al. 2019; Rawlik et al. 2023). A lot of light reaches during this time, which is necessary for the development of flowers and fruits (Stephenson 1981). The existence of many plant species, their biology, and their ecology depend on other organisms, e.g., pollinating insects (Kudo et al. 2008), which also have different activities depending on the seasons (Li et al. 2025). Seasonal changes in the species composition and biomass can vary strongly in individual habitats. The peak occurrence of geophytes occurs in spring, and summer is the period of dominance of species that tolerate shading better (Rawlik et al. 2023). However, little is known about how invasive trees, through the environmental changes they cause, can have a different impact on the biodiversity of the understory plants growing in temperate forests in spring and summer. Most previous studies focused mainly on summer vegetation, neglecting the spring aspect, abundant in forest specialists (Hermy et al. 1999).

Numerous previous studies proved that high biological diversity has a positive impact on the stability and durability of forest ecosystems (Hisano et al. 2018; Conradi et al. 2020). However, many works only discuss the issue of species richness. In addition to taxonomic diversity, which describes the number and abundance of species, it is worth delving deeper into the role of these species in ecosystems, related to their unique functional traits (functional diversity) (Violle et al. 2007), and the diversity of their evolutionary origins (phylogenetic diversity) (Tucker et

al. 2017). Functional and phylogenetic (Swenson and Enquist 2009) diversities (Violle et al. 2007; Laliberté and Legendre 2010; Hao et al. 2018) also indicate the resilience of the different components of ecosystems (Buckley et al. 2023).

Due to the large differences between nutrient-poor and nutrient-rich habitats in Central Europe, it is worth examining these habitats separately (Bury and Dyderski 2024b, 2025a). This will allow for better adaptation of protective treatments to the needs of specific plant communities (Nyssen and Vanhellemont 2016; Sádlo et al. 2017; Engel et al. 2024; Nyssen et al. 2024). Both of these habitats are characterized by a specific species composition. Plants adapted to the soil fertility grow there. Nutrient-poor stands are mostly dominated by coniferous trees, e.g., *P. sylvestris*, while nutrient-rich stands are dominated by deciduous trees, e.g., *Quercus* spp. However, these differences concern not only the tree stand level but also the understory vegetation (Ellenberg and Leuschner 2010; Mucina et al. 2016). In the context of invasion ecology, previous studies proved that changes caused by invasive woody species may be more negative in poor habitats (Chmura 2004; Halarewicz 2011), indicating context dependence (Novoa et al. 2020; Sapsford et al. 2020).

In this paper, we aimed to assess the impact of two invasive tree species, *P. serotina* and *R. pseudoacacia*, on understory vascular plant biodiversity at three levels: taxonomic, functional, and phylogenetic, as well as species composition. Furthermore, we assessed whether there are indicator species for increasing invader aboveground biomass. We hypothesized that (H1) we will find changes in vascular plant alpha diversity and species composition along invader aboveground biomass (Dickie et al. 2011; García et al. 2023; Bury and Dyderski 2024a). (H2) We hypothesized that the relationships between vascular plant diversity and invader biomass will be different between *P. serotina* and *R. pseudoacacia*, and additionally, we will find different taxa indicating invader aboveground biomass increase (Bury and Dyderski 2025a). (H3) Furthermore, we supposed that there will be differences in diversity-invader biomass relationships between nutrient-poor and nutrient-rich sites (Chmura 2004; Halarewicz 2011; Bury and Dyderski 2025a). (H4) Finally, we expected differences in patterns between spring and summer surveys. Checking the differences between spring, a season when many geophytes reach optimal growth, and summer–a season when different taxa (mostly hemicryptophytes) emerge (Rawlik et al. 2023)–should answer the question: which seasonal aspect of vegetation is more threatened by an increase in invasive tree biomass? We expect that in the spring, when canopy foliage has not yet emerged, the impact of the studied invasive trees will be lower (Heinrich 1976; Kudo et al. 2008; Czapiewska et al. 2019). Our work addresses an important and still poorly understood phenomenon called the per capita effect, or the scaled effect of invasion (Parker et al. 1999; Schooler et al. 2006; Bury and Dyderski 2024a). More specifically, in our research, we focus on aboveground biomass of invasive trees and how it affects the relationship between invasive trees and understory (Dickie et al. 2011; García et al. 2023; Bury and Dyderski 2024a). Additionally, we have placed our research in two contexts: habitat, which answers the question of where invasive species have a more or less significant impact, and seasonal, which answers the question of when the studied invasive species have a more or less significant impact on understory vegetation. The habitat context (Chmura 2004; Halarewicz 2011; Bury and Dyderski 2024a) is better known than the seasonal one. The seasonality we studied adds a novel perspective on the relationship between invasive trees and the understory vegetation.

Methods

Study design and study area

We conducted our study in the managed forests in Western Poland (Czerniejewo, Łopuchówko, Babki, Konstantynowo, and Jarocin Forest Districts (i.e., spatial administration units)). The climatic conditions are typical for a warm-summer humid continental climate with an annual temperature of 8.5 °C and mean annual precipitation of 500–550 mm (BDL 2024) (Suppl. material 1: fig. S1).

In the field, we searched for plots non-invaded (control) and invaded by *P. serotina* or *R. pseudoacacia*. Initially, we used canopy cover as an abundance indicator because it was easier to assess in the field and did not require time-consuming measurements necessary to estimate biomass. We used two classes of cover to distinguish plots with medium cover (< 30%) and high cover (> 50%), which formed the invasion gradient, based on species biomass. Additionally, we accounted for two different habitat and stand maturity contexts. We established our plots in nutrient-poor and nutrient-rich habitats. Nutrient-poor sites included plant communities dominated by *P. sylvestris*, i.e., *Leucobryo-Pinetum* W. Mat. (1962) 1973 communities or secondary *P. sylvestris* forests. Nutrient-rich sites included communities dominated by *Q. petraea* and *Q. robur*, i.e., different subtypes of *Galio sylvatici-Carpinetum betuli* Oberd. 1957 communities or secondary *Quercus* spp. forests (Bury and Dyderski 2025a). Some of our plots had characteristics of slightly poorer communities or slightly more fertile ones, e.g., *Potentillo albae-Quercetum* Libb. 1933 and *Querco-roboris Pinetum* Mat. et Polak. 1955 s.l. We also selected plots in two stand age classes. We distinguished medium-aged stands (stands in the middle of rotation age, 40–80 years old) and mature stands (close to rotation age; for Scots pines, 80–120 years old; for oaks, 100–140 years old). Medium-aged stands have simpler structures–trees have a similar diameter at breast height (DBH) and height–compared to more structurally diverse, mature stands. Mature stands grow more slowly than middle-aged stands because they have already reached the peak of growth (Jiang et al. 2017; Li et al. 2024). The older the tree stands, the greater the biodiversity, which is related to the greater availability of light correlated with the smaller stem density (Jagodziński and Oleksyn 2009; Felton et al. 2010; Conradi et al. 2020). In total, we established 160 plots (32 control plots, 64 plots with *R. pseudoacacia*, and 64 plots with *P. serotina*). To avoid the spatial autocorrelation, plots of individual variants were at least 5 km apart (plot variant = invader × invasion level × habitat × stand age) (Bury and Dyderski 2025a) (Fig. 1b).

Assessment of invader aboveground biomass

We assessed invader aboveground biomass using the same methodology as Bury and Dyderski (2025a, b). After an initial survey based on the cover of studied invasive species (subsection 2.1), we measured tree stand structures. We measured the DBH of all trees ≥ 1.3 m height on 102 plots in 2021 and 2022 (García et al. 2023; Bury and Dyderski 2025a). On the other 58 plots in 2022 and 2023, we measured the DBH of trees > 5 cm DBH, and we counted trees thinner than 5 cm. Then, we used the dataset for 102 plots, and for all tree species, we estimated the mean DBH for trees thinner than 5 cm (Bury and Dyderski 2025a) (Suppl. material 1: table S1). We decided to use this method to reduce time-consuming measurements of numerous thin individuals with low variability of DBH and not to assume a midpoint of DBH range from 0 to 5 cm (2.5 cm) for biomass calculation as in previous studies

(Dyderski and Jagodziński 2019). We used published allometric models (Suppl. material 1: table S2) to calculate invader aboveground biomass (Brown 1976; Alberti et al. 2005; Forrester et al. 2017; Zasada 2017; Jagodziński et al. 2018, 2019) (Fig. 2). *Prunus serotina* aboveground biomass on nutrient-poor sites ranged from 0.18 to 47.11 Mg ha^{-1} (mean: 7.34 ± 8.75 Mg ha^{-1}) and on nutrient-poor sites from 0.19 to 27.39 Mg ha^{-1} (mean: 6.68 ± 7.24 Mg ha^{-1}). *Robinia pseudoacacia* aboveground biomass on nutrient-poor sites ranged from 0.22 to 153 Mg ha^{-1} (mean: 20.91 ± 31.69 Mg ha^{-1}) and on nutrient-rich sites from 0.82 to 278.24 Mg ha^{-1} (mean: 50.77 ± 70.37 Mg ha^{-1}) (Suppl. material 1: table S4) (Bury and Dyderski 2025a).

Understory vegetation assessments

We used the modified nine-scaled Braun-Blanquet method (**r** – 1–2 ind.; **+** – <1%; **1** – 1–3%; **2m** – 3–10%; **2a** – 10–18%; **2b** – 18–25%; **3** – 25–50%; **4** – 50–75%; **5** – > 75%) to assess the cover of particular understory species of vascular plants. We assessed both herbaceous and woody plants (up to 0.5 m height) on four randomly distributed squared 25 m^2 subplots. We conducted an understory survey in the spring (May) and summer (July) of 2021, 2022, and 2023. We aggregated the results at the plot level by averaging species cover from four subplots (Fig. 2).

Alpha diversity indices calculation

In spring, we found 183 vascular plant species, while in summer, we found 167 (in total, 205 species). We calculated taxonomic alpha diversity using two indices: Shannon's diversity index, calculated by the diversity() function, and species richness, calculated by the specnumber() function, both from the vegan package (Oksanen et al. 2018). For phylogenetic alpha diversity, we calculated Faith's phylogenetic diversity (PD) and mean pairwise distance (MPD), using the ses.pd() and ses.mpd() functions from the picante package (Kambel et al. 2010). We acquired a phylogenetic tree by using the phylo.maker() function in the V.Phylomaker2 package (Jin and Qian 2022). Both PD and MPD were standardized to exclude

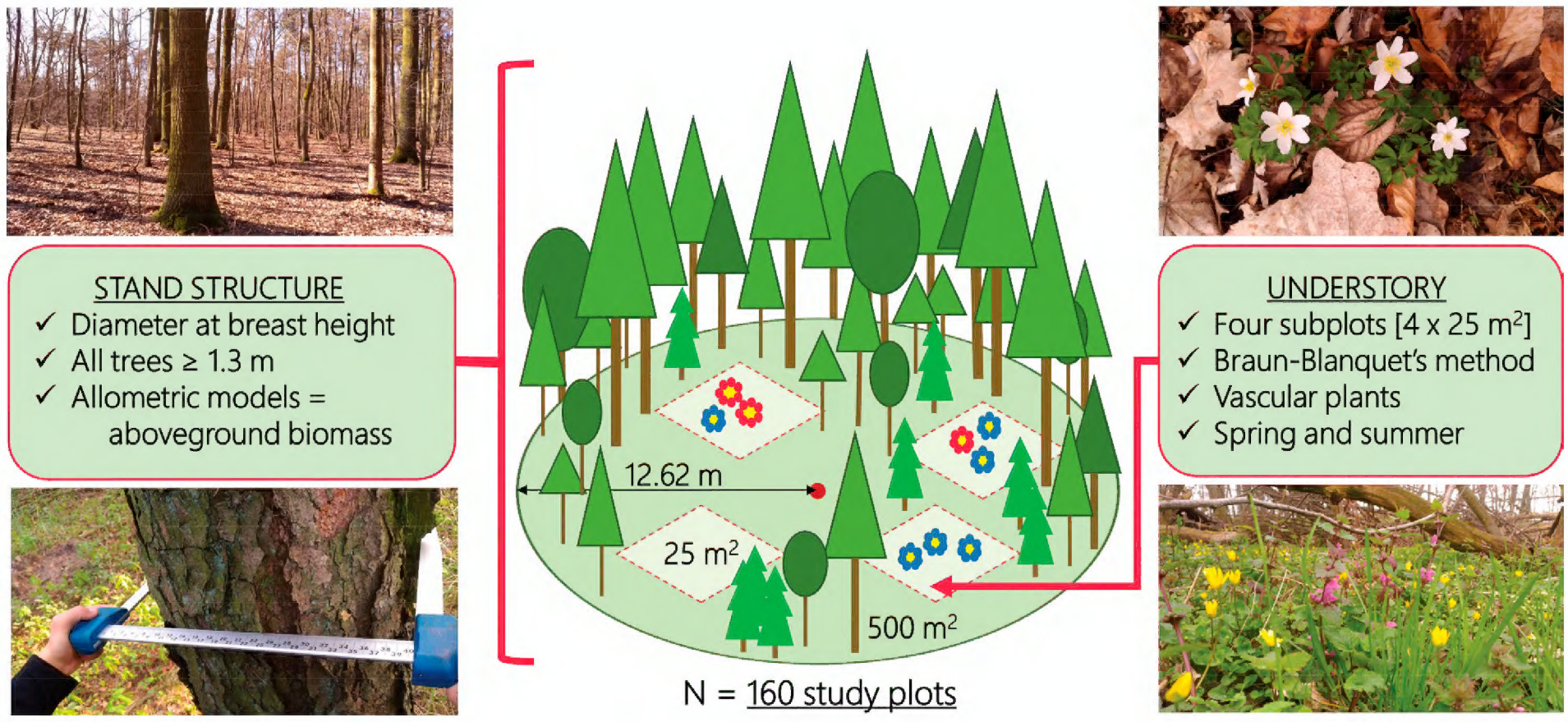

Figure 2. Graphical presentations of field surveys, including both stand structure measurements and understory vegetation surveys.

the effect of species richness on estimating phylogenetic diversity. For functional alpha diversity, we acquired functional traits for species present in our study plots from several databases, i.e., LEDA (Kleyer et al. 2008), BIEN (Maitner et al. 2018), BioFlor (Klotz et al. 2002), and Pladias (Wild et al. 2019). Additionally, we acquired ecological indicator values (EIVs) from Ellenberg and Leuschner (2010). Due to the low incompleteness of trait data (Suppl. material 1: table S5), we decided to impute missing values with the missForest package (Stekhoven and Buhlmann 2012), supported by phylogenetic eigenvectors (Diniz-Filho et al. 1998), calculated using the acquired phylogenetic tree. As functional diversity is species richness-dependent, we assessed the standardized (Czortek et al. 2021) functional richness (FRic) and functional dispersion (FDis), using the dbFD() function from the FD package (Laliberté and Legendre 2010). We followed the standardization algorithm provided by Czortek et al. (2021), where we calculated the null model based on species composition randomized using the randomizeMatrix() function from the picante package (Kambel et al. 2010) in 10000 iterations. The standardized indicator sesFRic was calculated using the formula: $sesFRic = FRic_R - FRic_{null}/SD(FRic_{null})$, where: $FRic_R$ is the observed *FRic* value, $FRic_{null}$ is the mean *FRic* value of the null model, and $SD(FRic_{null})$ is the standard deviation of the *FRic* null model. The standardized indicator *sesFDis* was calculated using the formula: $sesFDis = FDis_R - FDis_{null}/(FDis_{null})$, where: $FDis_R$ is the observed *FDis* value, $FDis_{null}$ is the mean *FDis* value of the null model, and $SD(FDis_{null})$ is the standard deviation of the *FDis* null model. As calculations of *FDis* and *FRic* are meaningful only for plant communities with at least three species, we excluded one plot for the spring dataset (control plot on nutrient-poor site) with only two species from analyses for these alpha diversity metrics. To characterize the functional composition of understory vegetation, we calculated community-weighted means (CWMs) of functional traits and EIVs: EIV.L – Light EIV; EIV.M – Moisture EIV; EIV.N – Soil Fertility EIV; EIV.SR – Soil Reaction EIV; SLA – Specific Leaf Area [$cm^2\ g^{-1}$]; H – Maximum height [m]; SM – Seed mass [mg].

Statistical analyses

From all analyses, we excluded one outlying study plot (nutrient-poor habitat) with *P. serotina* aboveground biomass (47.11 Mg ha^{-1}) tree times higher than the next plot in this variant (15.43), similarly to Bury and Dyderski (2025a). In all analyses we used log1p transformation (i.e., log(x+1)) of invader aboveground biomass to include sites with zero biomass and to stabilize variance in this predictor.

We used Canonical Correspondence Analysis (CCA) from the vegan package (Oksanen et al. 2018) to study the relationship between the studied invaders aboveground biomass and the vascular plant species composition of the understory. In CCA, we used invader aboveground biomass and stand age as constraints, testing the hypotheses about their impact on species composition. To test the significance of these factors, we used permutation-based ANOVA-like tests, implemented in the anova.cca() function.

We used the Threshold Indicator Taxa Analysis to check which species change their abundance over the studied invasive species biomass. We presented only those species that revealed trends with purity and reliability > 0.95 (default settings). We presented the results using the plottaxaridges() function from the TITAN2 package (Baker et al. 2023). This function creates graphs for particular species responses

along environmental gradients. These species are divided into two groups: increasers (different shapes of red color of ridges) and decliners (different shapes of grey color or blue color of ridges). The increasers are species with cover increasing with invader biomass increasing, while decliners are species with decreasing cover with invader biomass increasing. Ridges can look different for particular species. The inflection of the ridge indicates the value of the aboveground biomass of the invader where the cover of a particular species is the highest. A narrow ridge indicates small discrepancies in the data, and a wide ridge indicates large discrepancies. Z-values (numerical values that correspond to the intensity of ridge color) inform about the taxa indicator value–darker color and higher value suggest a higher indicator value. A vertical black line indicates aboveground biomass. In the case of increasers, there is a sharp increase in understory species cover, and in the case of decliners, there is a sharp decrease in understory species cover.

Finally, we used generalized linear mixed-effect models (GLMMs) (Brooks et al. 2017) to study the relationship between different invasive tree species aboveground biomass with alpha diversity metrics and CWMs of traits (SLA, SM, and H) and EIVs. In each model we also included stand age to control this variable. For each season, invasive tree species, and habitat, we developed separate models. For H and SM CWMs, we used log10 transformations of the dependent variable due to a high variability of these traits, exceeding four orders of magnitude. For species richness, we assumed a Poisson or negative binomial distribution, ensuring a lack of problems with overdispersion, while for all other variables, we assumed a Gaussian distribution due to the close-to-normal distribution of the dependent variable. We used the survey year and forest districts as random effects. We used the glmmTMB package (Brooks et al. 2017) to develop GLMMs and the dredge() function from the MuMIn package (Bartoń et al. 2017) to choose the best-fit models, reducing them to minimize values of Akaike's Information Criterion, corrected for small sample size (AICc). For each model, we stated the AICc of the final model and $AICc_0$, i.e., the AICc of the null (intercept and random effects-only model). We presented model responses using marginal responses, i.e., mean predicted values for each level of a particular predictor, calculated using the ggeffects package (Lüdecke 2018). In the results section, we present values estimated for statistically significant relationships for two points: for zero and near the maximum value of invader biomass in each variant. We used the same biomass values as in Bury and Dyderski (2025a). All mean values are followed by ± standard error.

Results

Relationships between invasive tree biomass and understory species composition

In spring we found a statistically significant relationship between species composition and invader aboveground biomass except for *R. pseudoacacia* on nutrient-rich sites (p=0.083; Fig. 3b, Table 1). On nutrient-poor sites, *Rubus idaeus*, *R. fruticosus* agg., and *P. serotina* increased their cover with an increase in *P. serotina* biomass (Fig. 3e), while species like *Moehringia trinervia*, *Fallopia convolvulus*, *Chelidonium majus*, *Impatiens parviflora*, *Geranium robertianum*, and *R. pseudoacacia* increased their cover with an increase in *R. pseudoacacia* biomass (Fig. 3a). For control plots

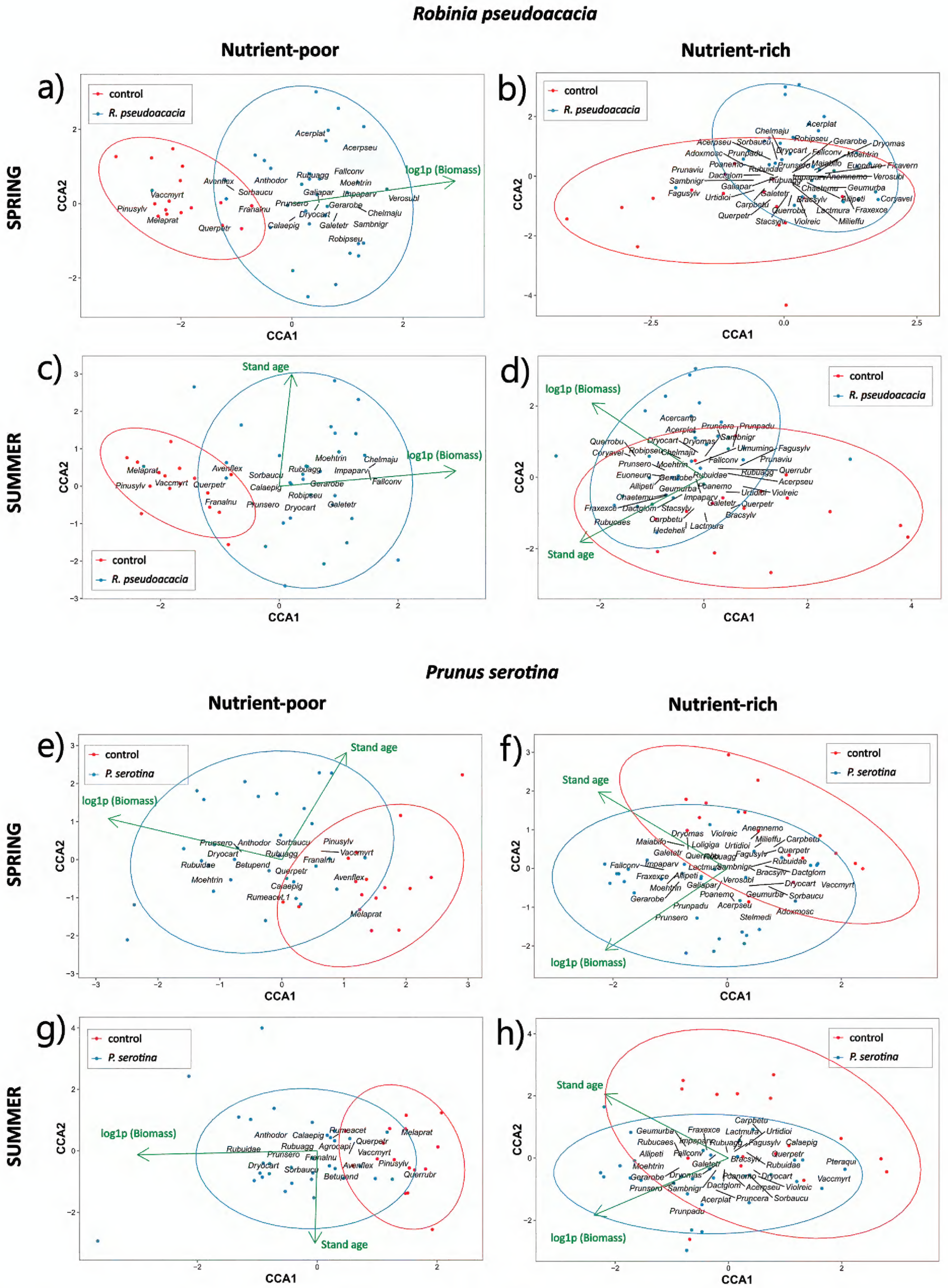

Figure 3. Canonical Correspondence Analysis (CCA) for all plot variants: *R. pseudoacacia* nutrient-poor (48 plots) and nutrient-rich sites (48 plots); *P. serotina* nutrient-rich (48 plots) and nutrient-poor sites (47 plots) for both spring and summer. For clarity, only species with a frequency > 20% were labeled. Green arrows and labels represent environmental variables (only for statistically significant results, $p < 0.05$). Red dots = control plots, blue dots = plots with *P. serotina* or *R. pseudoacacia*. Abbreviations: **log1p(Biomass)** – natural logarithm of invader aboveground biomass.

Table 1. Results of permutation-based ANOVA-like test (999 iterations) of constraint significance for CCA. Abbreviations: **log1p(Biomass)** – natural logarithm of invader aboveground biomass.

	Df	χ^2	F	Pr(>F)
SPRING				
P. serotina nutrient-poor sites (n = 47 plots)				
log1p(Biomass)	1	0.2098	2.2640	0.001
Stand age	1	0.1587	1.7132	0.012
Residual	44	4.0765		
P. serotina nutrient-rich sites (n = 48 plots)				
log1p(Biomass)	1	0.1484	1.4496	0.020
Stand age	1	0.1477	1.4421	0.017
Residual	45	4.6069		
R. pseudoacacia nutrient-poor sites (n = 48 plots)				
log1p(Biomass)	1	0.3038	2.7142	0.001
Stand age	1	0.1640	1.4656	0.122
Residual	45	5.0371		
R. pseudoacacia nutrient-rich sites (n = 48 plots)				
log1p(Biomass)	1	0.1408	1.2730	0.083
Stand age	1	1.1388	1.2545	0.105
Residual	45	4.9784		
SUMMER				
P. serotina nutrient-poor sites (n = 47 plots)				
log1p(Biomass)	1	0.1611	1.6468	0.007
Stand age	1	0.1444	1.4758	0.024
Residual	45	4.4022		
P. serotina nutrient-rich sites (n = 48 plots)				
log1p(Biomass)	1	0.2285	2.6348	0.001
Stand age	1	0.1339	1.5438	0.044
Residual	45	3.9033		
R. pseudoacacia nutrient-poor sites (n = 48 plots)				
log1p(Biomass)	1	0.3421	3.1727	0.001
Stand age	1	0.1839	1.7052	0.019
Residual	45	4.8252		
R. pseudoacacia nutrient-rich sites (n = 48 plots)				
log1p(Biomass)	1	0.1529	1.4946	0.017
Stand age	1	1.1520	1.4854	0.023
Residual	45	4.6044		

Abbreviations: **Df** – the degrees of freedom; χ^2 – Chi-squared statistics; **F** – F-statistics; **Pr(>F)** – p-values.

on nutrient-poor sites, *Vaccinium myrtillus*, *P. sylvestris*, and *Melampyrum pratense* were isolated on all graphs (Fig. 3a, e). On nutrient-rich sites, *P. serotina*, *G. robertianum*, *P. padus*, *M. trinervia*, and *Alliaria petiolata* increased their cover with an increase in *P. serotina* biomass (Fig. 3f). In summer, we found statistically significant relationships between species composition and invader biomass in all studied cases ($p < 0.01$; **T**able 1). On nutrient-poor sites, species like *Rubus idaeus*, *R. fruticosus* agg., and *P. serotina* increased their cover with increasing *P. serotina* biomass (Fig. 3g). On nutrient-poor sites, species like *M. trinervia*, *F. convolvulus*, *Ch. majus*, *I. parviflora*, and *G. robertianum* increased their cover with an increase in *R. pseudoacacia* biomass (Fig. 3c). For control plots on nutrient-poor

sites, *V. myrtillus*, *P. sylvestris*, and *M. pratense* are isolated on all graphs (Fig. 3c, g). On nutrient-rich sites, *Dryopteris carthusiana*, *R. pseudoacacia*, *P. serotina*, *M. trinervia*, *Acer campestre*, and *A. platanoides* increased their cover with an increase in *R. pseudoacacia* biomass (Fig. 3d). On nutrient-rich sites, *P. padus*, *G. robertianum*, *P. serotina*, *Sambucus nigra*, and *M. trinervia* increased their cover with an increase in *P. serotina* biomass (Fig. 3h).

Indicator taxa for invasive tree biomass

In spring, we detected decliners and increasers only on nutrient-rich sites with *P. serotina* (Fig. 4a, b, e, f; T Suppl. material 1: tables S6–S13). The cover of *Agrostis capillaris* decreased while the cover of *Corylus avellana* increased with an increase in invader biomass (Fig. 4f). In summer, in nutrient-poor habitats with *P. serotina*, we found five increasers: *I. parviflora*, *R. idaeus*, *D. carthusiana*, *P. serotina*, and *Rubus fruticosus* agg., and no decliners (Fig. 4g). In nutrient-rich habitats with *P. serotina*, we found three decliners: *Pteridium aquilinum*, *Oxalis acetosella*, and *Q. petraea*, and two increasers: *P. padus* and *P. serotina* (Fig. 4h). In nutrient-poor habitats with *R. pseudoacacia*, we found four decliners (*V. myrtillus*, *M. pratense*, *P. sylvestris*, and *Q. petraea*) and nine increasers: *S. nigra*, *Ch. majus*, *I. parviflora*, *F. convolvulus*, *M. trinervia*, *G. robertianum*, *D. carthusiana*, *R. fruticosus* agg., and *R. pseudoacacia* (Fig. 4c). In nutrient-rich habitats with *R. pseudoacacia*, we found one decliner (*Q. petraea*) and five increasers: *Q. robur*, *C. avellana*, *D. carthusiana*, *R. pseudoacacia*, and *Ch. majus* (Fig. 4d).

Relationship between invasive tree biomass and understory alpha diversity

On nutrient-poor sites in spring, we found a negative relationship between *R. pseudoacacia* aboveground biomass and mean pairwise distance (decreased from 0.26 ± 0.12 to – 0.39 ± 0.19 along an increase in invader biomass from 0 to 116 Mg ha^{-1}). Along this gradient, we found an increase in functional dispersion (from -0.53 ± 0.16 to 0.41 ± 0.25), moisture EIV (4.9 ± 0.1 to 5.5 ± 0.1), soil reaction EIV (6.5 ± 0.4 to 3.9 ± 0.2), SLA CWM (206.1 ± 20.3 cm^2 g^{-1} to 323.7 ± 32.6 cm^2 g^{-1}), and maximum height CWM (2.11 ± 0.09 m to 4.68 ± 0.13 m). In summer we found a higher species richness (11.0 ± 0.1 species to 21.3 ± 0.1 species), Shannon's diversity index (0.98 ± 0.14 to 1.91 ± 0.19), moisture EIV (4.8 ± 0.1 to 5.4 ± 0.1), soil fertility EIV (3.7 ± 0.2 to 6.6 ± 0.3), soil reaction EIV (3.2 ± 0.3 to 6.7 ± 0.4), and SLA CWM (202.8 ± 0.1 cm^2 g^{-1} to 383.0 ± 0.1 cm^2 g^{-1}) in plots with higher *P. serotina* biomass (Figs 5, 6, Suppl. material 1: tables S14, S18).

On nutrient-rich sites in spring, we found a positive relationship between *R. pseudoacacia* aboveground biomass and Faith's phylogenetic diversity (increased from -0.52 ± 0.20 to 0.08 ± 0.25 along an increase in invader biomass from 0 to 208 Mg ha^{-1}). Along this gradient, we found an increase in mean pairwise distance (from -0.56 ± 0.23 to 0.18 ± 0.27). In summer we found a decrease in functional dispersion (from -0.32 ± 0.13 to -0.98 ± 0.19) and an increase in Faith's phylogenetic diversity (from -0.35 ± 0.20 to 0.34 ± 0.25) with increasing *R. pseudoacacia* biomass (Figs 5, 6, Suppl. material 1: tables S15, S19).

On nutrient-poor sites in spring, we found a positive relationship between *P. serotina* aboveground biomass functional dispersion (from -0.60 ± 0.17 to 0.07 ±

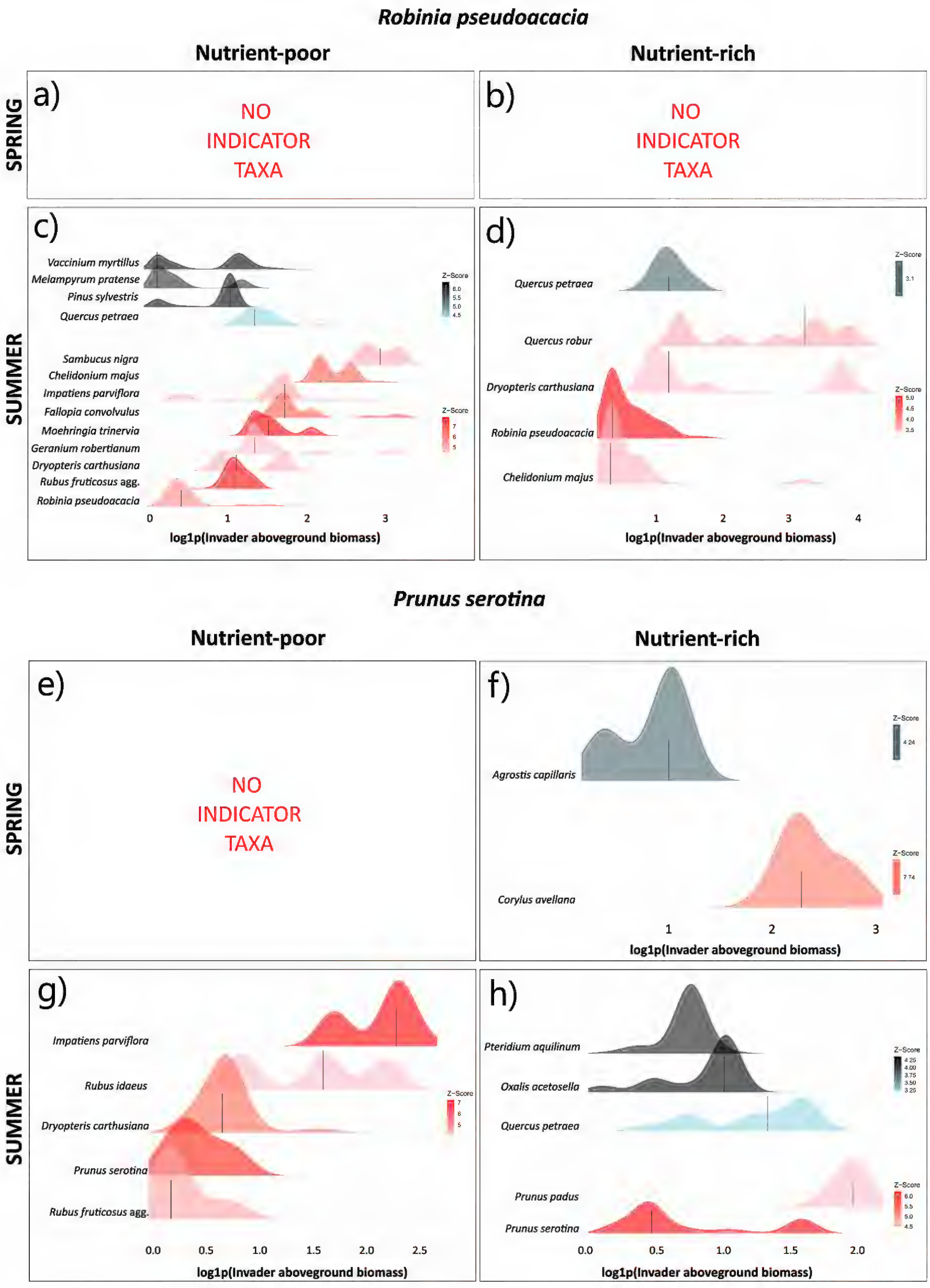

Figure 4. Results of the Threshold Indicator Taxa Analysis (see Methods section for graph interpretation) for all variants in both spring and summer: nutrient-poor sites with *P. serotina* (n = 47 plots), nutrient-rich sites with *P. serotina* (n = 48 plots), nutrient-poor sites with *R. pseudoacacia* (n = 48 plots), and nutrient-rich sites with *R. pseudoacacia* (n = 48 plots). Grey/light blue density estimators represent species responding negatively to the invader biomass gradient (decliners), while red color – positively (increasers). We included here only responses for species that were both reliable (reliability ≥ 0.95) and pure (purity ≥ 0.95). For statistics of all species, see Suppl. material 1: tables S6–S13.

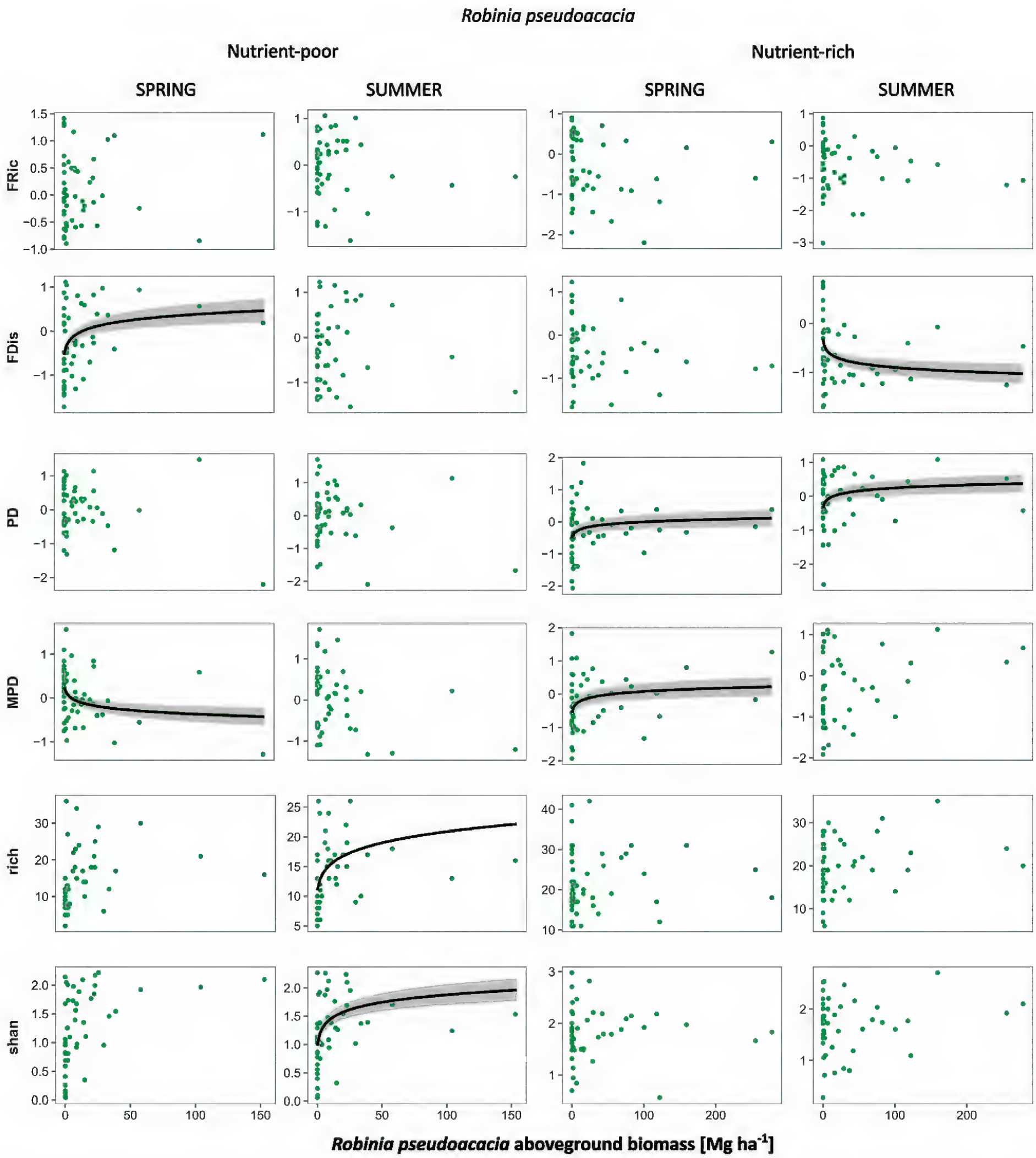

Figure 5. Generalized linear mixed-effect models for different plant diversity indicators depending on *Robinia pseudoacacia* aboveground biomass [Mg ha^{-1}] in both nutrient-poor and nutrient-rich sites in both spring and summer. Dark green dots – observed values; black line – marginal responses; grey area – marginal responses ± standard error. Marginal responses and marginal responses ± standard error only for statistically significant results. Abbreviations: **FRic** – SES Functional richness; **FDis** – SES Functional dispersion; **PD** – Faith's phylogenetic diversity; **MPD** – Mean Pairwise Distance; **rich** – Species richness; **shan** – Shannon's diversity index.

0.22) along with an increase in invader biomass from 0 to 16 Mg ha^{-1}. Along this gradient, we found an increase in species richness (from 9.6 ± 0.1 species to 13.7 ± 0.1 species), Shannon's diversity index (from 0.94 ± 0.22 to 1.43 ± 0.23), soil fertility EIV (from 3.6 ± 0.2 to 4.5 ± 0.3), soil reaction EIV increased (from 2.9 ± 0.3 to 4.9 ± 0.4), SLA CWM (from 197.2 ± 10.0 cm^2 g^{-1} to 240.6 ± 13.4 cm^2

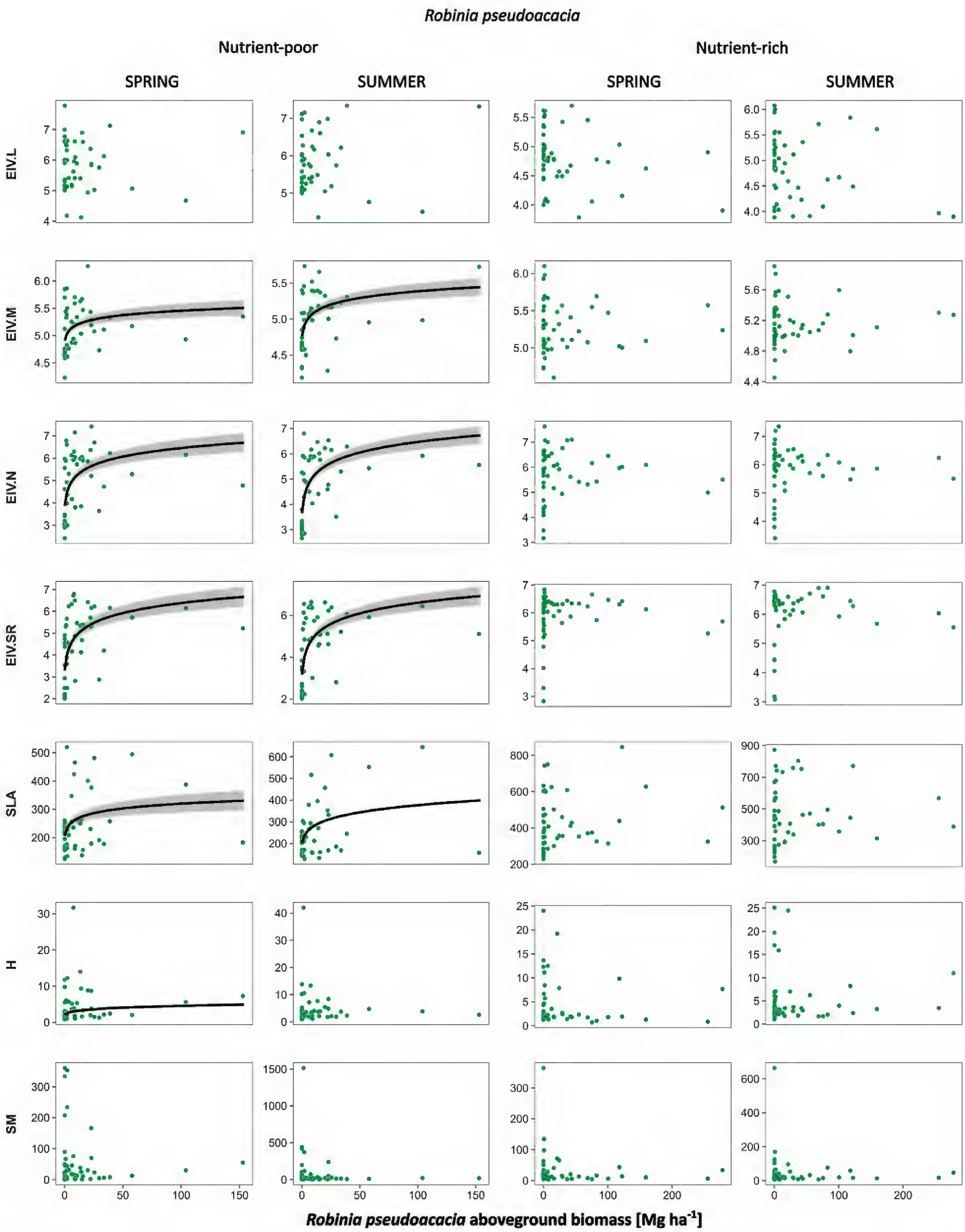

Figure 6. Generalized linear mixed-effect models for community-weighted means of functional traits and EIVs depending on *Robinia pseudoacacia* aboveground biomass [Mg ha^{-1}] in both nutrient-poor and nutrient-rich sites in both spring and summer. Dark green dots – observed values; black line – marginal responses; grey area – marginal responses ± standard error. Marginal responses and marginal responses ± standard error only for statistically significant results. Abbreviations: **EIV.L** – Light EIV; **EIV.M** – Moisture EIVe; **EIV.N** – Soil Fertility EIV; **EIV.SR** – Soil Reaction EIV; **SLA** – Specific Leaf Area CWM [cm^2 g^{-1}]; **H** – Maximum height CWM [m]; **SM** – Seed mass CWM [mg].

g^{-1}), and maximum height CWM (from 2.31 ± 0.07 m to 12.38 ± 0.09 m). In summer we found an increase in functional richness (from -0.02 ± 0.21 to 0.74 ± 0.23), species richness (from 9.9 ± 0.2 species to 14.0 ± 0.2 species), moisture EIV (from 4.7 ± 0.1 to 4.9 ± 0.1), soil fertility EIV (from 3.4 ± 0.2 to 4.6 ± 0.2), soil reaction EIV (from 2.9 ± 0.3 to 4.9 ± 0.3), and maximum height CWM (from 2.85 ± 0.11 m to 10.12 ± 0.11 m) with increasing invader biomass (Figs 7, 8, Suppl. material 1: tables S16, S20).

On nutrient-rich sites in spring, we found a positive relationship between *P. serotina* aboveground biomass and soil reaction EIV (increased from 5.5 ± 0.2 to 6.3 ± 0.3 along an increase in invader biomass from 0 to 28 Mg ha^{-1}). Along this gradient, we found an increase in maximum height CWM (from 2.79 ± 0.07 m to 6.79 ± 0.11 m) and SLA CWM (from 354.7 ± 25.7 cm^2 g^{-1} to 522.5 ± 42.4 cm^2 g^{-1}), with an increase in invader biomass. On nutrient-rich sites in summer, we did not find any statistically significant relationship between studied plant alpha diversity indicators, EIVs, and CWM of functional traits and *P. serotina* biomass (Figs 7, 8, Suppl. material 1: tables S17, S21).

Discussion

General patterns and species-specific trends

We confirmed the first and second hypotheses, revealing different relationships between alpha diversity and invader biomass for both studied neophytes. We found an overall increase in functional dispersion, species richness, and Shannon's index for both studied species in nutrient-poor sites, and an increase in phylogenetic diversity with increasing *R. pseudoacacia* biomass in nutrient-rich sites. Additionally, on nutrient-poor sites, we found an increase in functional richness for increasing biomass of *P. serotina* and a decrease in the mean pairwise distance for increasing biomass of *R. pseudoacacia*.

The relationship between invader biomass depended on particular diversity indices. We observed different indicator species for those two neophytes. In all CCA ordinations (Fig. 3) on nutrient-poor sites, we observed that these species were always associated with non-invaded plots: *V. myrtillus*, *P. sylvestris*, and *M. pratense*. These species are very important for natural coniferous forest communities in Central Europe, typical of *Dicrano-Pinion* W. Mat. 1962 alliance (Matuszkiewicz 2001). However, TITAN2 analysis confirms this negative relationship between invaders and these species only for nutrient-poor sites with *R. pseudoacacia* in summer (Fig. 4). *Vaccinium myrtillus*, *P. sylvestris*, and *M. pratense* prefer acidic soils, so their decreasing cover along the invader biomass can be caused by increasing soil pH and fertility, expressed by the increase in EIVs (Figs 6, 8). Also, Halarewicz and Pruchniewicz (2015) found a decrease in the frequency of the same species that, in our study, an increase in *P. serotina* cover, on nutrient-poor sites. A previous study (Woziwoda et al. 2021) confirmed the negative effect of invasive *Quercus rubra* presence on *V. myrtillus* cover in Scots pine forests, attributing this impact to decreasing light availability. This was in line with our observations. *Robinia pseudoacacia*, as a species with the ability to fix nitrogen, supplies large amounts of nitrogen into the soil (Danso et al. 1995; Noh et al. 2010), affecting species composition (Rice et al. 2004). This is in line with our observation of nitrophilous species such as *I. parviflora*, *G. robertianum*, or *M. trinervia*, where we observed

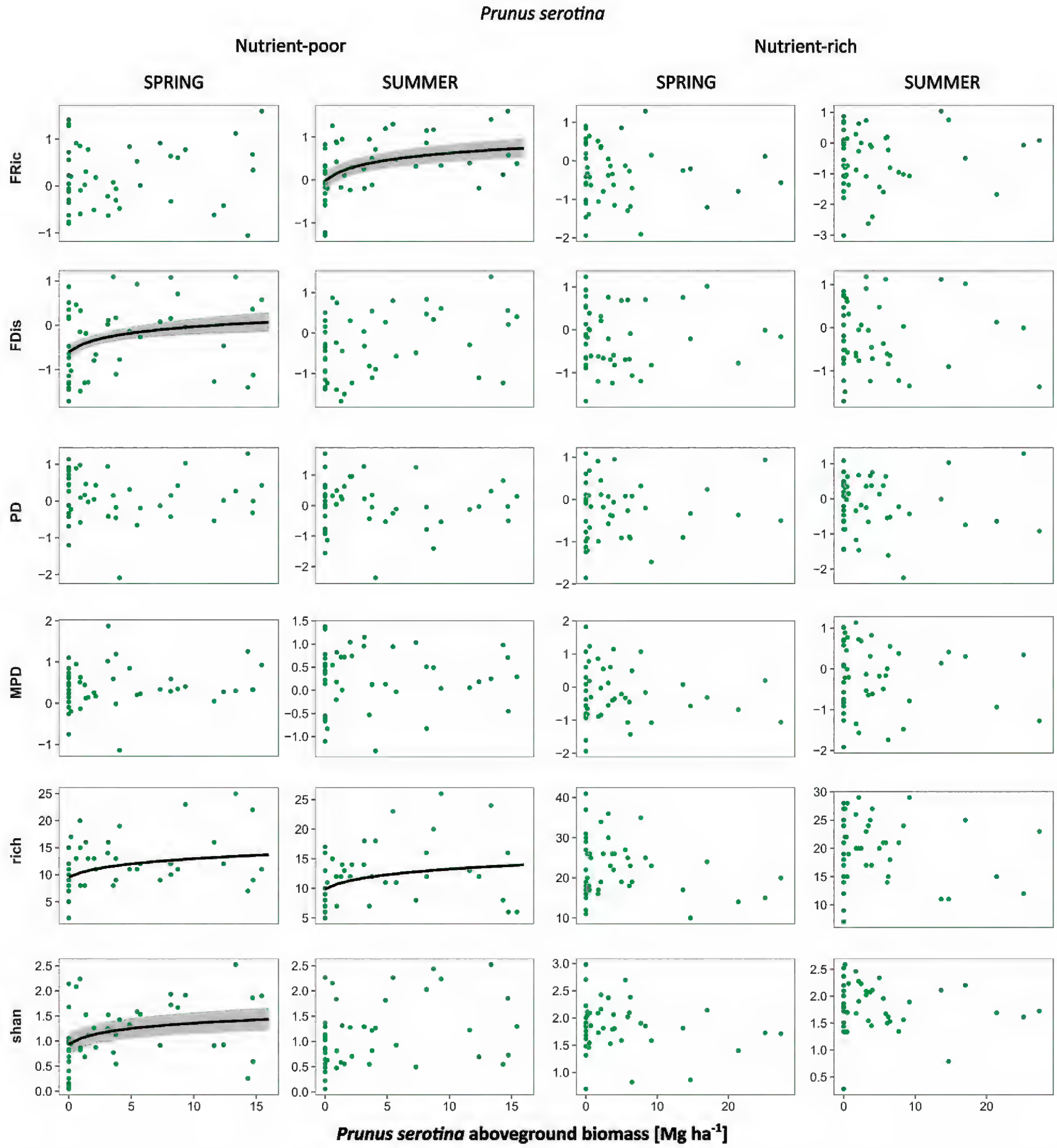

Figure 7. Generalized linear mixed-effect models for different plant diversity indicators depending on *Prunus serotina* aboveground biomass [Mg ha^{-1}] in both nutrient-poor and nutrient-rich sites in both spring and summer. Dark green dots – observed values; black line – marginal responses; grey area – marginal responses ± standard error. Marginal responses and marginal responses ± standard error only for statistically significant results. Abbreviations: **FRic** – SES Functional richness; **FDis** – SES Functional dispersion; **PD** – Faith's phylogenetic diversity; **MPD** – Mean Pairwise Distance; **rich** – Species richness; **shan** – Shannon's diversity index.

a positive relationship between their cover and invader biomass. These species are known to respond positively to nitrogen deposition (Perring et al. 2018). Similarly, Halarewicz and Pruchniewicz (2015) found an increase in *I. parviflora* frequency with increasing *P. serotina* cover. Despite a different nitrogen management strategy than *R. pseudoacacia*, *P. serotina* also supplies a large amount of this element into the soil (Aerts et al. 2017; Horodecki et al. 2019).

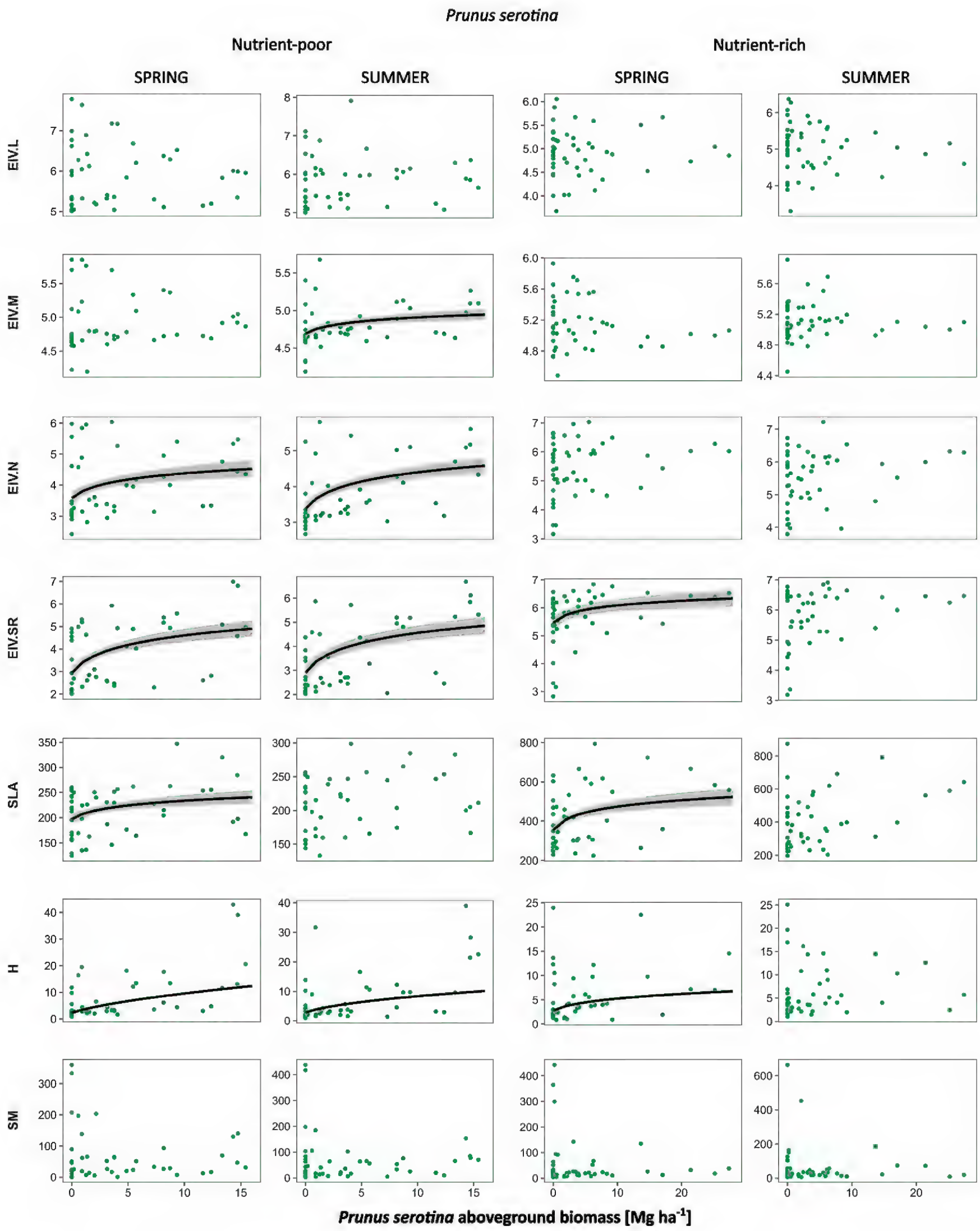

Figure 8. Generalized linear mixed-effect models for community-weighted means of functional traits and EIVs depending on *Prunus serotina* aboveground biomass [Mg ha^{-1}] in both nutrient-poor and nutrient-rich sites in both spring and summer. Dark green dots – observed values; black line – marginal responses; grey area – marginal responses ± standard error. Marginal responses and marginal responses ± standard error only for statistically significant results. Abbreviations: **EIV.L** – Light EIV; **EIV.M** – Moisture EIV; **EIV.N** – Soil Fertility EIV; **EIV.SR** – Soil Reaction EIV; **SLA** – Specific Leaf Area CWM [cm^2 g^{-1}]; **H** – Maximum height CWM [m]; **SM** – Seed mass CWM [mg].

Previous studies about both *P. serotina* (Chabrerie et al. 2008, 2010) and *R. pseudoacacia* (Montecchiari et al. 2020) per capita effect on understory biodiversity focused on the cover as an abundance metric. Chabrerie et al. (2010), examining the overstory dominance of *P. serotina*, showed that more specialized species were in

invaded stands, and the species richness and vegetation cover were lower, in contrast to our study. Traits describing shade tolerance, ruderal plants with a short life cycle, and geophytes were associated with invaded habitats, and light-demanding species were associated with non-invaded stands. Chabrerie et al. (2008) showed that the communities of herbaceous species differed slightly between those with *P. serotina* and those without. The trend observed in Chabrerie et al. (2008) is therefore opposite to ours. In our study, true forest species were more associated with areas with lower invader biomass, and with the increasing amount of invader biomass, the coverage of ruderal and edge species increased (e.g., *Rubus* spp. in nutrient-poor habitats invaded by *P. serotina*, *I. parviflora*, *G. robertianum*, or *M. trinervia* in nutrient-poor habitats invaded by *R. pseudoacacia*), while forest specialists decreased (e.g., *P. sylvestris* and *V. myrtillus* in nutrient-poor habitats with *R. pseudoacacia*). These differences may result from local environmental conditions and different species compositions of stands. In our study, we had either pine or oak stands. Chabrerie et al. (2008) assessed mixed stands with beech, oak, and pine in a single large forest complex (14,417 ha). Our plots were in various scattered forest complexes, from very small (approx. 12 ha) to large, compact complexes (approx. 15,000 ha–Zielonka Forest). In contrast to our results, Montecchiari et al. (2020) confirm that *R. pseudoacacia* increasing cover increased the presence of alien species and nitrophilous species and decreased Shannon's diversity index in *Quercus pubescens* sub-Mediterranean forests. Šibíková et al. (2019) showed that in the invaded stands dominated by *R. pseudoacacia*, there were more common generalists, and the pool of species decreased from 442 to 372 species compared to the native nutrient-rich (oak forests, oak-hornbeam forests, and hardwood floodplain forests) forests. For *R. pseudoacacia* stands, they found many nitrophilous species, e.g., *Ch. majus*, *S. nigra*, *Geum urbanum*, and heliophilous grasses, e.g., *Arrhenatherum elatius*, similarly to our study. Slabejová et al. (2023) showed that stands invaded by *R. pseudoacacia* were characterized by greater availability of light on the forest floor, higher temperature, and lower humidity. In the understory, increasing coverage of ruderal, non-forest species and a greater share of alien species were observed in comparison to native stands. However, native stands differed in terms of changes caused by the replacement by *R. pseudoacacia*. Floodplain forests were less affected than mixed oak-hornbeam forests. As floodplain forests are more fertile than oak-hornbeam forests, this trend is in line with our results, indicating higher resistance of nutrient-rich habitats.

Context dependence and biotic resistance

Previous studies confirmed differences between nutrient-poor and nutrient-rich habitats in relationships between invasive trees and plant diversity (H3). They revealed both positive (Von Holle et al. 2013; Gentili et al. 2019; Bury and Dyderski 2024a) and negative (Godefroid et al. 2005; Trentanovi et al. 2013; Lazzaro et al. 2018; Gentili et al. 2019; Kowarik et al. 2019; Montecchiari et al. 2020) effects of studied invaders on taxonomic alpha diversity, while most of them showed insignificant relationships (e.g., Verheyen et al. 2007; Hejda et al. 2017; Sitzia et al. 2018; Gentili et al. 2019; Slabejová et al. 2019). However, most of them focused on nutrient-rich sites. Only five focused on nutrient-poor sites (Verheyen et al. 2007; Halarewicz 2012; Halarewicz and Żołnierz 2014; Dyderski and Jagodziński 2021; Bury and Dyderski 2024a). In our study, the increase in taxonomic diversity was statistically significant only in the nutrient-poor sites (Figs 5, 7). However,

the number of species does not describe the quality of species composition. In our study, in nutrient-poor habitats, the relationships between invader biomass and the CWMs of EIV.M, EIV.N, and EIV.SR increased with invader biomass increase (Figs 6, 8). These results might indicate transformations of case soil characteristics by invaders (Danso et al. 1995; Noh et al. 2010; Aerts et al. 2017; Kato-Noguchi and Kato 2024). This may be related to the emergence of species that prefer more fertile and alkaline soils and may promote forest generalists, leading to the decline of forest specialists (Woziwoda et al. 2014, 2019; Slabejová et al. 2019; Šibíková et al. 2019). The decrease and increase in species cover are reflected in differences in the individual alpha diversity indices of each type.

In nutrient-poor habitats, FDis increases with increasing invader biomass. In the nutrient-rich habitats, on the other hand, for summer, FDis decreased for *R. pseudoacacia* (Fig. 5). The observed increase in functional diversity for *R. pseudoacacia* can be explained by the expansion of ruderal, edge, and nitrophilous species in sites dominated by acidophilous species. That way, invaded communities comprise species from both groups, enriching the set of functional traits and their diversity. This condition is caused by the enrichment of soil in a nutrient-rich leaf litter (Rice et al. 2004; Horodecki et al. 2019) of *R. pseudoacacia*, which increases soil pH and fertility. The same processes can explain the increase in FDis in nutrient-poor habitats with *P. serotina*.

The decline in the mentioned functional diversity indicators in a nutrient-rich habitat is slightly more difficult to interpret. These habitats are naturally characterized by higher diversity. The changes in EIVs caused by the presence of *R. pseudoacacia* on nutrient-rich sites were statistically insignificant. In our previous study, conducted in Wielkopolska National Park, about the per capita effect (based on aboveground biomass proportion of *P. serotina* in total biomass) of *P. serotina* invasion on understory alpha diversity, we found a positive relationship between total species richness (+ 8.8 species) and functional richness (+ 0.08) along proportion of *P. serotina* in stand biomass ranging from 0 to 10%. However, we investigated this relationship in natural *P. sylvestris* stands and nutrient-rich sites with artificially planted *P. sylvestris*. In this study we noticed that light played a significant role as a driver of changes, and both the understory plants and the *P. serotina* itself benefited from the higher availability of light. Dyderski and Jagodziński (2021) showed that *P. sylvestris* plantations (on fertile soils) invaded by *P. serotina* have one-fourth higher species richness than non-invaded ones, and non-invaded *P. sylvestris* stands (on nutrient-poor soils) had 13% more species than those invaded by *P. serotina*, while *Quercus-Acer-Tilia* stands (similar to our control stands on nutrient-rich sites) had 15% lower species richness than *R. pseudoacacia* stands. Thus, in a previous study, we found higher functional alpha diversity in *P. sylvestris* stands invaded by *P. serotina* than in non-invaded stands and higher in *R. pseudoacacia* stands than in *Quercus-Acer-Tilia* stands (Dyderski and Jagodziński 2021).

The increase in both MPD and PD in the forest habitat with *R. pseudoacacia* suggests that the number of evolutionary pathways, expressed by tree branches, is higher in more invaded sites. This may result from the fact that emerging species are more diverse in terms of phylogeny than the plants present in the ecosystem before invasion. In turn, the decreasing number of forest specialists in nutrient-poor habitats with *R. pseudoacacia*, representing different clades, e.g., *V. myrtillus* and *M. pratense*, or *P. sylvestris*, with the simultaneous introduction of nitrophilous generalists with closer phylogeny might lead to a decrease in MPD. These differences between nutrient-rich and nutrient-poor habitats can be explained by Piwczyński et al.'s (2016)

study. They proved that different alien species can shape the relationship between phylogenetic variability and the presence of an alien species in different ways. Additionally, the authors proved that environmental conditions, i.e., soil pH and light availability, were more important in shaping phylogenetic diversity than dominant tree species. This explains why we observed a different reaction in the nutrient-poor and forest habitats where the transformations of conditions were stronger, which is reflected in the significant results for EIVs. The mechanisms responsible for the species composition of the community can be explained by their phylogenetic structure. Environmental filtering, i.e., when species with similar ecological features can survive in unfavorable conditions, can lead to phylogenetic attraction. On the other hand, phylogenetic overdispersion indicates the dominant importance of interspecific competition. In such a situation, phylogenetically distinct species with different ecological features dominate in a given community. Our study plots were characterized by different intensities of invasion. In the early phases of invasion, characterized by greater environmental instability, we observed the advantage of clustering associated with the action of environmental filtration. In the later stages of invasion, stability increases and interspecific competition increases at the same time, leading to phylogenetic overdispersion (Webb et al. 2002). Other authors confirm that the phylogenetic structure of communities can change along the environmental gradient (Webb and Peart 2000; Cavender-Bares and Holbrook 2001). Our previous studies are in line with new results: Dyderski and Jagodziński (2021) found a higher phylogenetic diversity in *P. sylvestris* stands invaded by *P. serotina* than in non-invaded stands. The phylogenetic diversity was higher in *R. pseudoacacia* stands than in control *Quercus-Acer-Tilia* stands. Confirming the same trends using a quantitative gradient of invasive tree abundance in managed forests highlights the generality of discovered patterns. However, previous studies focused more on taxonomic and functional diversity, not allowing us a wider comparison of these trends.

Seasonality

Our results partially supported the fourth hypothesis. In spring we found species related to invader biomass gradient only on nutrient-rich sites with *P. serotina* (two species), with no indicator species in other variants. We expected that the presence of *R. pseudoacacia* and *P. serotina*, especially *R. pseudoacacia* in the overstory in nutrient-rich habitats, would significantly affect spring species. Compared to native oaks, *R. pseudoacacia* transmits more light through to the forest floor (Slabejová et al. 2019, 2023) and also develops foliage later than native oaks. This could create favorable conditions for the development of geophytes–a group of plants that are an important element of the species composition in spring in oak-hornbeam forests (Rawlik et al. 2023). Perhaps due to their ephemeral nature, these plants are less threatened by disturbances related to the presence and transformation of invasive species, because changes in soil chemistry are not so significant in fertile habitats. What is more interesting, according to our results, is that in both summer and spring (for *R. pseudoacacia*), the light EIV (Fig. 6) suggests better conditions for shade-tolerant species. In turn, in summer there were many more of these species. Some of the species were present in both seasons; however, there were differences in their cover, especially of the geophytes. In spring, some understory species have already started to grow, so their cover is low. Therefore, it is difficult to clearly state to what extent the lack of indicator species depends on the actual relationship of invaders with the understory, or whether in general the statis-

tical power of analyses based on the spring dataset is too low. Comparing spring and summer responses, observed on CCA graphs (Fig. 3), we can find that *M. trinervia*, *F. convolvulus*, *Ch. majus*, *I. parviflora*, *R. pseudoacacia*, and *G. robertianum* are typical of sites with higher *R. pseudoacacia* biomass. This may indicate the high population stability of these species in nutrient-poor habitats with *R. pseudoacacia*. *Fallopia convolvulus*, *Ch. majus*, and *I. parviflora* are nitrophilous, ruderal species, peculiar to habitats transformed by different human activities, while *M. trinervia* is an edge species more typical for forest edges (Ratyńska et al. 2010; Mucina et al. 2016). The same trend (according to CCA spring vs. summer) was observed for stands with *P. serotina* for *R. idaeus*, *R. fruticosus* agg., and *P. serotina*. We obtained very similar results comparing spring and summer for species richness (increase; Fig. 5) for *P. serotina* on nutrient-poor habitats and PD (increase; Fig. 7) for *R. pseudoacacia* on nutrient-rich habitats (Fig. 5). It is difficult to determine what accounts for the consistency or divergence between individual indicators for spring and summer. It may be related to the presence or absence of tree leaves in particular seasons (Heinrich 1976; Kudo et al. 2008; Rawlik et al. 2023). There may be a difference between spring and summer in the context of resource use by plants and seasonal differences in resource availability (Tonkin et al. 2017; Yan et al. 2023). It can determine the impact or lack of impact in spring or summer, and individual alpha diversity indices are characterized by different stability, e.g., the total number of species will change, but their functional features or phylogeny are not significantly different from those of species present before the invasion. However, seasonality in the context of studying the impact of tree invasions, especially scaled effects, on the understory is not well understood.

Forest understory vegetation conservation and invasive tree management

The potential effect of ecosystem transformations of *P. serotina* and *R. pseudoacacia* seems to be more visible and stronger in nutrient-poor habitats. This is important in the context of protecting habitats for acidophilous plants. Our study shows that the relationship between acidophilous species cover and invader biomass is negative. Of course, we studied semi-natural managed forests. However, if we apply the above premise to valuable, protected forests, we may fear that acidophilous, protected, and rare species may also poorly tolerate the growing biomass of *R. pseudoacacia* and *P. serotina*. Our study showed that it is very important to look deeper into biodiversity, not only focusing on numbers–total species richness–but also on species structure–particular species abundance–in particular habitat types and seasons. *Vaccinium myrtillus* is a very important component of nutrient-poor forest vegetation in Central and Northern Europe (Ritchie 1956). A serious question that can be asked based on our results is whether the sacrifice of dominant species important for coniferous habitats can be sacrificed in the name of increasing species richness. Perhaps more studies are needed to assess even more precisely in what configurations this wealth will decrease. A better assessment of the scaled effect at higher levels of diversity, e.g., gamma biodiversity, is also needed. Changes in nutrient-rich habitats are less intensive than in the case of nutrient-poor habitats. This is consistent with previous works by various authors (Chmura 2004; Halarewicz 2011; Bury and Dyderski 2025a, b). In these habitats, maintaining and improving the resistance of native habitats is crucial. This can be achieved by supporting the addition of native tree species that tolerate competition from the studied invasive species

(Nyssen and Vanhellemont 2016; Sádlo et al. 2017). There are various methods of preventing and combating invasive tree species. Unfortunately, sometimes the eradication of invasive trees can complicate management (Namura-Ochalska and Borowa 2015; Nyssen et al. 2024). For both *P. serotina* (Nyssen and Vanhellemont 2016) and *R. pseudoacacia* (Sádlo et al. 2017), management should be specific to the habitat and protection status of a given forest area (Nyssen and Vanhellemont 2016; Sádlo et al. 2017). As Sádlo et al. (2017) emphasize for *R. pseudoacacia*, various stakeholders should be reconciled to reach a compromise between different ecological and economic values. Increasing resistance might include decreasing forest patch invasibility by maintaining a closed canopy or decreasing propagule pressure by eliminating reproducing specimens of invasive trees in the surroundings.

Conclusion

We confirmed that the impacts of two invasive species, *P. serotina* and *R. pseudoacacia*, on species composition and alpha diversity of the understory scale with invader biomass. We also showed differences in impacts between habitats and seasons. We found various spring and summer indicator species for *P. serotina* and *R. pseudoacacia* quantity in nutrient-poor habitats dominated by *P. sylvestris* and nutrient-rich habitats dominated by *Q. petraea*/*robur*. Additionally, we showed that *P. serotina* and *R. pseudoacacia* had different relationships between their biomass and various indicators of taxonomic, functional, and phylogenetic diversity in particular habitats and seasons. Especially on nutrient-poor sites, we can see that ruderal and forest edge species increased their cover with invader biomass increasing, while forest specialists typical for those habitats decreased their cover. Due to the protection of natural habitats for acidophilous plants, the decreasing coverage of specialists, more noticeable for stands with *R. pseudoacacia* in our study, is worrying. These results confirm that we should focus more attention on nutrient-poor habitats and increase the resistance of these stands to invasion, and this should apply to stands with different functions and different protection regimes. Our results draw attention to the complex issue of the presence of invasive trees in forest ecosystems, and we proved that the relationship between invader biomass and understory vegetation is context-dependent. Field observations, their analysis, and their interpretation enrich our knowledge and should contribute to better management of invasive tree species and better protection of semi-natural and natural ecosystems. It is worth examining biodiversity at many levels and examining the impact of invasive trees in different habitats and seasons. It is also important to study not only the presence or absence of invaders but also the effect on their biomass.

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Additional information

Conflict of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

Ethical statement

The study did involve human or animal participants as study subjects. Authors obtained consent for fieldwork from the respective State Forest Districts.

Use of AI

Authors declare that AI was not used for the research and manuscript preparation.

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Author contributions

Conceptualization: SB, MKD; methodology: SB, MKD; investigation: SB, MKD; formal analysis: SB; visualization: SB; writing–original draft preparation: SB; writing–review and editing: MKD; funding acquisition: MKD.

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Data availability

All data supporting the results are archived in the Figshare repository (10.6084/m9.figshare.28494962). For review purposes, please use the following link: https://figshare.com/s/8de871c9063c8ff4b600.

References

Aerts R, Ewald M, Nicolas M, Piat J, Skowronek S, Lenoir J, Hattab T, Garzón-López CX, Feilhauer H, Schmidtlein S, Rocchini D, Decocq G, Somers B, Van De Kerchove R, Denef K, Honnay O (2017) Invasion by the Alien Tree *Prunus serotina* Alters Ecosystem Functions in a Temperate Deciduous Forest. Frontiers in Plant Science 8. https://doi.org/10.3389/fpls.2017.00179

Alberti G, Candido P, Peressotti A, Turco S, Piussi P, Zerbi G (2005) Aboveground biomass relationships for mixed ash (*Fraxinus excelsior* L. and *Ulmus glabra* Hudson) stands in Eastern Prealps of Friuli Venezia Giulia (Italy). Annals of Forest Science 62: 831–836. https://doi.org/10.1051/forest:2005089

Baker M, King R, Kahle D (2023) TITAN2: Threshold Indicator Taxa Analysis. R package version 2.4.3. https://CRAN.R-project.org/package=TITAN2

Bartoń K (2017) MuMIn: Multi-Model Inference. https://cran.r-project.org/web/packages/MuMIn/index.html

BDL (2024) Bank Danych o Lasach. https://www.bdl.lasy.gov.pl/portal/mapy-en [Accessed 06 August 2024]

Benesperi R, Giuliani C, Zanetti S, Gennai M, Mariotti Lippi M, Guidi T, Nascimbene J, Foggi B (2012) Forest plant diversity is threatened by *Robinia pseudoacacia* (black-locust) invasion. Biodiversity and Conservation 21: 3555–3568. https://doi.org/10.1007/s10531-012-0380-5

Bouteiller XP, Bussolo M, Ségura R, Mariette S, Porté AJ (2023) Considering both sexual and clonal reproduction could help loosen the conflict of use over *Robinia pseudoacacia*. Dendrobiology 90: 30–38. https://doi.org/10.12657/denbio.090.002

Brondízio ES, Settele J, Díaz S, Ngo HT [Eds] (2019) The global assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), Bonn.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9(2): 378–400. https://doi.org/10.32614/RJ-2017-066

Brown JK (1976) Estimating shrub biomass from basal stem diameters. Canadian Journal of Forest Research 6(2): 153–158. https://doi.org/10.1139/x76-019

Brus R, Pötzelsberger E, Lapin K, Brundu G, Orazio C, Straigyte L, Hasenauer H (2019) Extent, distribution and origin of non-native forest tree species in Europe. Scandinavian Journal of Forest Research 34: 533–544. https://doi.org/10.1080/02827581.2019.1676464

Buckley HL, Hall D, Jarvis RM, Smith V, Walker LA, Silby J, Hinchliffe G, Stanley MC, Sweeney AP, Case BS (2023) Using long-term experimental restoration of agroecosystems in Aotearoa New Zealand to improve implementation of Nature-based Solutions for climate change mitigation. Frontiers in Forests and Global Change 5: e950041. https://doi.org/10.3389/ffgc.2022.950041

Bury S, Dyderski MK (2024a) In search of *per capita* effects of *Prunus serotina* Ehrh. invasion on temperate forest understory alpha diversity. Biologia 79: 3011–3025. https://doi.org/10.1007/s11756-024-01766-7

Bury S, Dyderski MK (2024b) No effect of invasive tree species on aboveground biomass increments of oaks and pines in temperate forests. Forest Ecosystems 11: e100201. https://doi.org/10.1016/j.fecs.2024.100201

Bury S, Dyderski MK (2025a) Invasive *Prunus serotina* vs. *Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity? NeoBiota 97: 179–213. https://doi.org/10.3897/neobiota.97.135421

Bury S, Dyderski MK (2025b) Invasive tree species affect terricolous bryophytes biomass and biodiversity in nutrient-poor but not nutrient-rich temperate forests. Scientific Reports 15: e5272. https://doi.org/10.1038/s41598-025-89917-x

Cavender-Bares J, Holbrook NM (2001) Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats. Plant, Cell & Environment 24: 1243–1256. https://doi.org/10.1046/j.1365-3040.2001.00797.x

Chabrerie O, Verheyen K, Saguez R, Decocq G (2008) Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest: Invasion-disturbance-ecosystem interactions. Diversity & Distributions 14: 204–212. https://doi.org/10.1111/j.1472-4642.2007.00453.x

Chabrerie O, Loinard J, Perrin S, Saguez R, Decocq G (2010) Impact of *Prunus serotina* invasion on understory functional diversity in a European temperate forest. Biological Invasions 12: 1891–1907. https://doi.org/10.1007/s10530-009-9599-9

Chmura D (2004) Penetration and naturalisation of invasive alien plant species (neophytes) in woodlands of the Silesian Upland (Southern Poland). Nature Conservation 60: 3–11.

Cierjacks A, Kowarik I, Joshi J, Hempel S, Ristow M, Von Der Lippe M, Weber E (2013) Biological Flora of the British Isles: *Robinia pseudoacacia*. Journal of Ecology 101: 1623–1640. https://doi.org/10.1111/1365-2745.12162

Closset-Kopp D, Chabrerie O, Valentin B, Delachapelle H, Decocq G (2007) When Oskar meets Alice: Does a lack of trade-off in r/K-strategies make *Prunus serotina* a successful invader of European forests? Forest Ecology and Management 247: 120–130. https://doi.org/10.1016/j.foreco.2007.04.023

Conradi T, Van Meerbeek K, Ordonez A, Svenning J (2020) Biogeographic historical legacies in the net primary productivity of Northern Hemisphere forests. Ecology Letters 23: 800–810. https://doi.org/10.1111/ele.13481

Corenblit D, Steiger J, Tabacchi E, González E, Planty-Tabacchi A-M (2014) Ecosystem engineers modulate exotic invasions in riparian plant communities by modifying hydrogeomorphic

connectivity: Ecosystem engineers modulate exotic invasions. River Research and Applications 30: 45–59. https://doi.org/10.1002/rra.2618

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. Oikos 97: 153–166. https://doi.org/10.1034/j.1600-0706.2002.970201.x

Czapiewska N, Dyderski MK, Jagodziński AM (2019) Seasonal dynamics of floodplain forest understory–Impacts of degradation, light availability and temperature on biomass and species composition. Forests 10: 1–22. https://doi.org/10.3390/f10010022

Czortek P, Orczewska A, Dyderski MK (2021) Niche differentiation, competition or habitat filtering? Mechanisms explaining co-occurrence of plant species on wet meadows of high conservation value. Journal of Vegetation Science 32: e12983. https://doi.org/10.1111/jvs.12983

Danso SKA, Zapata F, Awonaike KO (1995) Measurement of biological N_2-fixation in field-grown *Robinia pseudoacacia* L. Soil Biology & Biochemistry 27: 415–419. https://doi.org/10.1016/0038-0717(95)98612-R

Deckers B, Verheyen K, Vanhellemont M, Maddens E, Muys B, Hermy M (2008) Impact of avian frugivores on dispersal and recruitment of the invasive *Prunus serotina* in an agricultural landscape. Biological Invasions 10: 717–727. https://doi.org/10.1007/s10530-007-9164-3

Dickie IA, Yates GW, John MGSt, Stevenson BA, Scott JT, Rillig MC, Peltzer DA, Orwin KH, Kirschbaum MUF, Hunt JE, Burrows LE, Barbour MM, Aislabie J (2011) Ecosystem service and biodiversity trade-offs in two woody successions. Journal of Applied Ecology 48: 926–934. https://doi.org/10.1111/j.1365-2664.2011.01980.x

Diniz-Filho JAF, de Sant'Ana CER, Bini LM (1998) An eigenvector method for estimating phylogenetic inertia. Evolution; International Journal of Organic Evolution 52: 1247–1262. https://doi.org/10.1111/j.1558-5646.1998.tb02006.x

Dyderski MK, Jagodziński AM (2019) Similar Impacts of Alien and Native Tree Species on Understory Light Availability in a Temperate Forest. Forests 10: e951. https://doi.org/10.3390/f10110951

Dyderski MK, Jagodziński AM (2021) Impacts of invasive trees on alpha and beta diversity of temperate forest understories. Biological Invasions 23: 235–252. https://doi.org/10.1007/s10530-020-02367-6

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. UTB, Stuttgart.

Engel M, Nyssen B, Desie E, Den Ouden J, Raats L, Hagemann U (2024) Managing Black Cherry (*Prunus serotina* Ehrh.) in European Forests: Insights from native and non-native ranges. Forest Ecology and Management 562: e121959. https://doi.org/10.1016/j.foreco.2024.121959

Felton A, Lindbladh M, Brunet J, Fritz Ö (2010) Replacing coniferous monocultures with mixed-species production stands: An assessment of the potential benefits for forest biodiversity in northern Europe. Forest Ecology and Management 260: 939–947. https://doi.org/10.1016/j.foreco.2010.06.011

Forrester DI, Tachauer IHH, Annighoefer P, Barbeito I, Pretzsch H, Ruiz-Peinado R, Stark H, Vacchiano G, Zlatanov T, Chakraborty T, Saha S, Sileshi GW (2017) Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. Forest Ecology and Management 396: 160–175. https://doi.org/10.1016/j.foreco.2017.04.011

García RA, Fuentes-Lillo E, Cavieres L, Cóbar-Carranza AJ, Davis KT, Naour M, Núñez MA, Maxwell BD, Lembrechts JJ, Pauchard A (2023) *Pinus contorta* Alters Microenvironmental Conditions and Reduces Plant Diversity in Patagonian Ecosystems. Diversity 15. https://doi.org/10.3390/d15030320

Gentili R, Ferrè C, Cardarelli E, Montagnani C, Bogliani G, Citterio S, Comolli R (2019) Comparing Negative Impacts of *Prunus serotina*, *Quercus rubra* and *Robinia pseudoacacia* on Native Forest Ecosystems. Forests 10: e842. https://doi.org/10.3390/f10100842

Godefroid S, Phartyal SS, Weyembergh G, Koedam N (2005) Ecological factors controlling the abundance of non-native invasive black cherry (*Prunus serotina*) in deciduous forest understory in Belgium. Forest Ecology and Management 210: 91–105. https://doi.org/10.1016/j.foreco.2005.02.024

Halarewicz A (2011) The reasons underlying the invasion of forest communities by black cherry, *Prunus serotina* and its subsequent consequences. Forest Research Papers 72: 267–272. https://doi.org/10.2478/v10111-011-0026-5

Halarewicz A (2012) Właściwości Ekologiczne i Skutki Rozprzestrzeniania się Czeremchy Amerykańskiej *Padus serotina* (Ehrh.) Borkh. w wybranych fitocenozach leśnych. Wydawnictwo Uniwersytetu Przyrodniczego, Wrocław, 143 pp.

Halarewicz A, Pruchniewicz D (2015) Vegetation and environmental changes in a Scots pine forest invaded by *Prunus serotina*: What is the threat to terricolous bryophytes? European Journal of Forest Research 134: 793–801. https://doi.org/10.1007/s10342-015-0890-2

Halarewicz A, Żołnierz L (2014) Changes in the understorey of mixed coniferous forest plant communities dominated by the American black cherry (*Prunus serotina* Ehrh.). Forest Ecology and Management 313: 91–97. https://doi.org/10.1016/j.foreco.2013.11.006

Hao M, Zhang C, Zhao X, Von Gadow K (2018) Functional and phylogenetic diversity determine woody productivity in a temperate forest. Ecology and Evolution 8: 2395–2406. https://doi.org/10.1002/ece3.3857

Heberling JM, Cassidy ST, Fridley JD, Kalisz S (2019) Carbon gain phenologies of spring-flowering perennials in a deciduous forest indicate a novel niche for a widespread invader. The New Phytologist 221: 778–788. https://doi.org/10.1111/nph.15404

Heinrich G (1976) Flowering phenologies: Bog, woodland, anddisturbed habitats. Ecology 57: 890–899. https://doi.org/10.2307/1941055

Hejda M, Hanzelka J, Kadlec T, Štrobl M, Pyšek P, Reif J (2017) Impacts of an invasive tree across trophic levels: Species richness, community composition and resident species' traits. Diversity and Distributions 23: 997–1007. https://doi.org/10.1111/ddi.12596

Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson JE (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biological Conservation 91: 9–22. https://doi.org/10.1016/S0006-3207(99)00045-2

Hisano M, Searle EB, Chen HYH (2018) Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. Biological Reviews of the Cambridge Philosophical Society 93: 439–456. https://doi.org/10.1111/brv.12351

Horodecki P, Nowiński M, Jagodziński AM (2019) Advantages of mixed tree stands in restoration of upper soil layers on postmining sites: A five-year leaf litter decomposition experiment. Land Degradation & Development 30: 3–13. https://doi.org/10.1002/ldr.3194

Jagodziński AM, Oleksyn J (2009) Ecological consequences of silviculture at variable stand densities. III. Stand stability, phytoclimate and biodiversity. Sylwan 153: 219–230.

Jagodziński AM, Dyderski MK, Gęsikiewicz K, Horodecki P (2018) Tree- and Stand-Level Biomass Estimation in a *Larix decidua* Mill. Chronosequence. Forests 9: e587. https://doi.org/10.3390/f9100587

Jagodziński AM, Dyderski MK, Gęsikiewicz K, Horodecki P (2019) Effects of stand features on aboveground biomass and biomass conversion and expansion factors based on a *Pinus sylvestris* L. chronosequence in Western Poland. European Journal of Forest Research 138: 673–683. https://doi.org/10.1007/s10342-019-01197-z

Jagodziński AM, Horodecki P, Jasińska AK, Maliński T, Pilarek Z, Woźniak K, Wrońska-Pilarek D, Zieliński J, Dyderski MK (2024) Invasive × *Sorbaronia fallax* nothosubsp. *mitschurinii* affects temperate Scots pine forest biodiversity and functioning. Forest Ecology and Management 568: e122147. https://doi.org/10.1016/j.foreco.2024.122147

Jiang P, Chen Y, Cao Y (2017) C:N:P Stoichiometry and Carbon Storage in a Naturally-Regenerated Secondary *Quercus variabilis* Forest Age Sequence in the Qinling Mountains, China. Forests 8: e281. https://doi.org/10.3390/f8080281

Jin Y, Qian H (2022) V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. Plant Diversity 44: 335–339. https://doi.org/10.1016/j.pld.2022.05.005

Kambel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly SP, Blomberg SP, Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26: 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kato-Noguchi H, Kato M (2024) Invasive Characteristics of *Robinia pseudoacacia* and Its Impacts on Species Diversity. Diversity 16: e773. https://doi.org/10.3390/d16120773

Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, van Groenendael JM, Klimeš L, Klimešová J, Klotz S, Rusch GM, Hermy M, Adriaens D, Boedeltje G, Bossuyt B, Dannemann A, Endels P, Götzenberger L, Hodgson JG, Jackel A-K, Kühn I, Kunzmann D, Ozinga WA, Römermann C, Stadler M, Schlegelmilch J, Steendam HJ, Tackenberg O, Wilmann B, Cornelissen JHC, Eriksson O, Garnier E, Peco B (2008) The LEDA Traitbase: A database of life-history traits of the Northwest European flora. Journal of Ecology 96: 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Klotz S, Kühn I, Durka W (2002) BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde. Bundesamt für Naturschutz, Bonn.

Kowarik I, Hiller A, Planchuelo G, Seitz B, Von Der Lippe M, Buchholz S (2019) Emerging Urban Forests: Opportunities for Promoting the Wild Side of the Urban Green Infrastructure. Sustainability 11: e6318. https://doi.org/10.3390/su11226318

Kudo G, Ida TY, Tani T (2008) Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants. Ecology 89: 321–331. https://doi.org/10.1890/06-2131.1

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91: 299–305. https://doi.org/10.1890/08-2244.1

Langmaier M, Lapin K (2020) A Systematic review of the impact of invasive alien plants on forest regeneration in european temperate forests. Frontiers in Plant Science 11: e524969. https://doi.org/10.3389/fpls.2020.524969

Lazzaro L, Mazza G, d'Errico G, Fabiani A, Giuliani C, Inghilesi AF, Lagomarsino A, Landi S, Lastrucci L, Pastorelli R, Roversi PF, Torrini G, Tricarico E, Foggi B (2018) How ecosystems change following invasion by *Robinia pseudoacacia*: Insights from soil chemical properties and soil microbial, nematode, microarthropod and plant communities. The Science of the Total Environment 622–623: 1509–1518. https://doi.org/10.1016/j.scitotenv.2017.10.017

Li Z, Mao C, Wu Q, Peng Y, Wang J, Zhang B, Zhang S, Liang X, Yan W, Chen X (2024) Temporal Variations in Aboveground Biomass, Nutrient Content, and Ecological Stoichiometry in Young and Middle-Aged Stands of Chinese Fir Forests. Plants 13: e1877. https://doi.org/10.3390/plants13131877

Li D, Belitz M, Campbell L, Guralnick R (2025) Extreme weather events have strong but different impacts on plant and insect phenology. Nature Climate Change. https://doi.org/10.1038/s41558-025-02248-7

López-Núñez FA, Heleno RH, Ribeiro S, Marchante H, Marchante E (2017) Four-trophic level food webs reveal the cascading impacts of an invasive plant targeted for biocontrol. Ecology 98(3): 782–793. https://doi.org/10.1002/ecy.1701

Lüdecke D (2018) ggeffects: Tidy data frames of marginal effects from regression models. Journal of Open Source Software 3: e772. https://doi.org/10.21105/joss.00772

Maitner BS, Boyle B, Casler N, Condit R, Donoghue J, Durán SM, Guaderrama D, Hinchliff CE, Jørgensen PM, Kraft NJB, McGill B, Merow C, Morueta-Holme N, Peet RK, Sandel B, Schild-

hauer M, Smith SA, Svenning J, Thiers B, Violle C, Wiser S, Enquist BJ (2018) The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database. Methods in Ecology and Evolution 9: 373–379. https://doi.org/10.1111/2041-210X.12861

Martin GD (2019) Addressing geographical bias: A review of *Robinia pseudoacacia* (black locust) in the Southern Hemisphere. South African Journal of Botany 125: 481–492. https://doi.org/10.1016/j.sajb.2019.08.014

Matuszkiewicz W (2001) Przewodnik do oznaczania zbiorowisk roślinnych Polski. Wydawnictwo Naukowe PWN.

Miller JR, White HP, Chen JM, Peddle DR, McDermid G, Fournier RA, Shepherd P, Rubinstein I, Freemantle J, Soffer R, LeDrew E (1997) Seasonal change in understory reflectance of boreal forests and influence on canopy vegetation indices. Journal of Geophysical Research, D, Atmospheres 102: 29475–29482. https://doi.org/10.1029/97JD02558

Montecchiari S, Tesei G, Allegrezza M (2020) Effects of *Robinia pseudoacacia* coverage on diversity and environmental conditions of central-northern Italian *Quercus pubescens* sub-Mediterranean forests (habitat code 91AA*): a threshold assessment. Annali di Botanica: 33–54. https://doi.org/10.13133/2239-3129/16447

Mucina L, Bültmann H, Dierßen K, Theurillat J, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, García RG, Chytrý M, Hájek M, Di Pietro R, Iakushenko D, Pallas J, Daniëls FJA, Bergmeier E, Santos Guerra A, Ermakov N, Valachovič M, Schaminée JHJ, Lysenko T, Didukh YP, Pignatti S, Rodwell JS, Capelo J, Weber HE, Solomeshch A, Dimopoulos P, Aguiar C, Hennekens SM, Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19: 3–264. https://doi.org/10.1111/avsc.12257

Namura-Ochalska A, Borowa B (2015) Walka z czeremchą amerykańską *Padus serotina* (Ehrh.) Borkh. w leśnictwie Rózin w Kampinoskim Parku Narodowym; ocena skuteczności wybranych metod. In: Krzysztofiak L, Krzysztofiak A (Eds) Inwazyjne Gatunki Obcego Pochodzenia Zagrożeniem dla rodzimej Przyrody red. Stowarzyszenie "Człowiek i Przyroda," Krzywe, 127–142.

Noh NJ, Son Y, Koo JW, Seo KW, Kim RH, Lee YY, Yoo KS (2010) Comparison of nitrogen fixation for North- and South-facing *Robinia pseudoacacia* stands in Central Korea. Journal of Plant Biology 53: 61–69. https://doi.org/10.13133/2239-3129/16447

Novoa A, Richardson DM, Pyšek P, Meyerson LA, Bacher S, Canavan S, Catford JA, Čuda J, Essl F, Foxcroft LC, Genovesi P, Hirsch H, Hui C, Jackson MC, Kueffer C, Le Roux JJ, Measey J, Mohanty NP, Moodley D, Müller-Schärer H, Packer JG, Pergl J, Robinson TB, Saul W-C, Shackleton RT, Visser V, Weyl OLF, Yannelli FA, Wilson JRU (2020) Invasion syndromes: A systematic approach for predicting biological invasions and facilitating effective management. Biological Invasions 22: 1801–1820. https://doi.org/10.1007/s10530-020-02220-w

Nyssen B, Vanhellemont M (2016) 5.6 Integrating black cherry in forest management in the Netherlands and Belgium. In: Krumm F, Vítková L (Eds) Introduced Tree Species in European Forests: Opportunities and Challenges. European Forest Institute, 362–372.

Nyssen B, Ouden JD, Bindewald A, Brancalion P, Kremer K, Lapin K, Raats L, Schatzdorfer E, Stanturf J, Verheyen K, Muys B (2024) Established Invasive Tree Species Offer Opportunities for Forest Resilience to Climate Change. Current Forestry Reports 10: 456–486. https://doi.org/10.1007/s40725-024-00232-6

Oksanen J, Blanchet F, Kindt R (2018) vegan 2.3.3. – Community Ecology Package. http://CRAN.R-project.org/package=vegan

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: Toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3–19. https://doi.org/10.1023/A:1010034312781

Perring MP, Diekmann M, Midolo G, Schellenberger Costa D, Bernhardt-Römermann M, Otto JCJ, Gilliam FS, Hedwall P-O, Nordin A, Dirnböck T, Simkin SM, Máliš F, Blondeel H, Brunet J, Chudomelová M, Durak T, De Frenne P, Hédl R, Kopecký M, Landuyt D, Li D, Manning P, Petřík P, Reczyńska K, Schmidt W, Standovár T, Świerkosz K, Vild O, Waller DM, Verheyen K (2018) Understanding context dependency in the response of forest understorey plant communities to nitrogen deposition. Environmental Pollution 242: 1787–1799. https://doi.org/10.1016/j.envpol.2018.07.089

Piwczyński M, Puchałka R, Ulrich W (2016) Influence of tree plantations on the phylogenetic structure of understorey plant communities. Forest Ecology and Management 376: 231–237. https://doi.org/10.1016/j.foreco.2016.06.011

Qiu L, Zhang X, Cheng J, Yin X (2010) Effects of black locust (*Robinia pseudoacacia*) on soil properties in the loessial gully region of the Loess Plateau, China. Plant and Soil 332: 207–217. https://doi.org/10.1007/s11104-010-0286-5

Rahmonov O (2009) The Chemical Composition of Plant Litter of Black Locust (*Robinia pseudoacacia* L.) and Its Ecological Role in Sandy Ecosystems. Shengtai Xuebao. Acta Ecologica Sinica 29: 237–243. https://doi.org/10.1016/j.chnaes.2009.08.006

Ratyńska H, Wojterska M, Brzeg A, Kołacz M (2010) Multimedialna Encyklopedia Zbiorowisk Roślinnych Polski.

Rautiainen M, Mõttus M, Heiskanen J, Akujärvi A, Majasalmi T, Stenberg P (2011) Seasonal reflectance dynamics of common understory types in a northern European boreal forest. Remote Sensing of Environment 115: 3020–3028. https://doi.org/10.1016/j.rse.2011.06.005

Rawlik K, Rawlik M, Jagodziński AM (2023) Seasonal dynamics of herbaceous layer biomass and its contribution to annual net primary production in an oak–hornbeam forest. Forest Ecology and Management 544: e121195. https://doi.org/10.1016/j.foreco.2023.121195

Rice SK, Westerman B, Federici R (2004) Impacts of the Exotic, Nitrogen-Fixing Black Locust (*Robinia pseudoacacia*) on Nitrogen- Cycling in a Pine-Oak Ecosystem. Plant Ecology 174: 97–107. https://doi.org/10.1023/B:VEGE.0000046049.21900.5a

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: Concepts and definitions. Diversity & Distributions 6: 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Ritchie JC (1956) *Vaccinium myrtillus* L. Journal of Ecology 44: e291. https://doi.org/10.2307/2257181

Roy HE, Pauchard A, Stoett PJ, Renard Truong T, Meyerson LA, Bacher S, Galil BS, Hulme PE, Ikeda T, Kavileveettil S, McGeoch MA, Nuñez MA, Ordonez A, Rahlao SJ, Schwindt E, Seebens H, Sheppard AW, Vandvik V, Aleksanyan A, Ansong M, August T, Blanchard R, Brugnoli E, Bukombe JK, Bwalya B, Byun C, Camacho-Cervantes M, Cassey P, Castillo ML, Courchamp F, Dehnen-Schmutz K, Zenni RD, Egawa C, Essl F, Fayvush G, Fernandez RD, Fernandez M, Foxcroft LC, Genovesi P, Groom QJ, González AI, Helm A, Herrera I, Hiremath AJ, Howard PL, Hui C, Ikegami M, Keskin E, Koyama A, Ksenofontov S, Lenzner B, Lipinskaya T, Lockwood JL, Mangwa DC, Martinou AF, McDermott SM, Morales CL, Müllerová J, Mungi NA, Munishi LK, Ojaveer H, Pagad SN, Pallewatta NPKTS, Peacock LR, Per E, Pergl J, Preda C, Pyšek P, Rai RK, Ricciardi A, Richardson DM, Riley S, Rono BJ, Ryan-Colton E, Saeedi H, Shrestha BB, Simberloff D, Tawake A, Tricarico E, Vanderhoeven S, Vicente J, Vilà M, Wanzala W, Werenkraut V, Weyl OLF, Wilson JRU, Xavier RO, Ziller SR (2024) Curbing the major and growing threats from invasive alien species is urgent and achievable. Nature Ecology & Evolution 8: 1216–1223. https://doi.org/10.1038/s41559-024-02412-w

Sádlo J, Vítková M, Pergl J, Pyšek P (2017) Towards site-specific management of invasive alien trees based on the assessment of their impacts: The case of *Robinia pseudoacacia*. NeoBiota 35: 1–34. https://doi.org/10.3897/neobiota.35.11909

Sapsford SJ, Brandt AJ, Davis KT, Peralta G, Dickie IA, Gibson RD, Green JL, Hulme PE, Nuñez MA, Orwin KH, Pauchard A, Wardle DA, Peltzer DA (2020) Towards a framework for under-

standing the context dependence of impacts of non-native tree species. Functional Ecology 34: 944–955. https://doi.org/10.1111/1365-2435.13544

Schooler SS, McEvoy PB, Coombs EM (2006) Negative per capita effects of purple loosestrife and reed canary grass on plant diversity of wetland communities. Diversity & Distributions 12: 351–363. https://doi.org/10.1111/j.1366-9516.2006.00227.x

Šibíková M, Jarolímek I, Hegedüšová K, Májeková J, Mikulová K, Slabejová D, Škodová I, Zaliberová M, Medvecká J (2019) Effect of planting alien *Robinia pseudoacacia* trees on homogenization of Central European forest vegetation. The Science of the Total Environment 687: 1164–1175. https://doi.org/10.1016/j.scitotenv.2019.06.043

Sitzia T, Campagnaro T, Kotze DJ, Nardi S, Ertani A (2018) The invasion of abandoned fields by a major alien tree filters understory plant traits in novel forest ecosystems. Scientific Reports 8: e8410. https://doi.org/10.1038/s41598-018-26493-3

Slabejová D, Bacigál T, Hegedüšová K, Májeková J, Medvecká J, Mikulová K, Šibíková M, Škodová I, Zaliberová M, Jarolímek I (2019) Comparison of the understory vegetation of native forests and adjacent *Robinia pseudoacacia* plantations in the Carpathian-Pannonian region. Forest Ecology and Management 439: 28–40. https://doi.org/10.1016/j.foreco.2019.02.039

Slabejová D, Čejka T, Hegedüšová K, Májeková J, Medvecká J, Mikulová K, Šibíková M, Škodová I, Šustek Z, Jarolímek I (2023) Comparison of alien *Robinia pseudoacacia* stands with native forest stands across different taxonomic groups. Forest Ecology and Management 548: e121413. https://doi.org/10.1016/j.foreco.2023.121413

Starfinger U, Kowarik I, Rode M, Schepker H (2003) From desirable ornamental plant to pest to accepted addition to the flora? – The perception of an alien tree species through the centuries. Biological Invasions 5: 323–335. https://doi.org/10.1023/B:BINV.0000005573.14800.07

Stekhoven DJ, Buhlmann P (2012) MissForest–non-parametric missing value imputation for mixed-type data. Bioinformatics 28: 112–118. https://doi.org/10.1093/bioinformatics/btr597

Stephenson AG (1981) Flower and fruit abortion: Proximate causes and ultimate functions. Annual Review of Ecology and Systematics 12: 253–279. https://doi.org/10.1146/annurev.es.12.110181.001345

Swenson NG, Enquist BJ (2009) Opposing assembly mechanisms in a Neotropical dry forest: Implications for phylogenetic and functional community ecology. Ecology 90: 2161–2170. https://doi.org/10.1890/08-1025.1

Tonkin JD, Bogan MT, Bonada N, Rios-Touma B, Lytle DA (2017) Seasonality and predictability shape temporal species diversity. Ecology 98: 1201–1216. https://doi.org/10.1002/ecy.1761

Trentanovi G, Ziechmann U, Kowarik I, Cierjacks A (2013) Biotic homogenization at the community scale: Disentangling the roles of urbanization and plant invasion. Diversity & Distributions 19(7): 738–748. https://doi.org/10.1111/ddi.12028

Tucker CM, Cadotte MW, Carvalho SB, Davies TJ, Ferrier S, Fritz SA, Grenyer R, Helmus MR, Jin LS, Mooers AO, Pavoine S, Purschke O, Redding DW, Rosauer DF, Winter M, Mazel F (2017) A guide to phylogenetic metrics for conservation, community ecology and macroecology: A guide to phylogenetic metrics for ecology. Biological Reviews of the Cambridge Philosophical Society 92: 698–715. https://doi.org/10.1111/brv.12252

Verheyen K, Vanhellemont M, Stock T, Hermy M (2007) Predicting patterns of invasion by black cherry (*Prunus serotina* Ehrh.) in Flanders (Belgium) and its impact on the forest understorey community. Diversity & Distributions 13: 487–497. https://doi.org/10.1111/j.1472-4642.2007.00334.x

Vilà M, Trillo A, Castro-Díez P, Gallardo B, Bacher S (2024) Field studies of the ecological impacts of invasive plants in Europe. NeoBiota 90: 139–159. https://doi.org/10.3897/neobiota.90.112368

Violle C, Navias M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116: 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Vítková M, Müllerová J, Sádlo J, Pergl J, Pyšek P (2017) Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. Forest Ecology and Management 384: 287–302. https://doi.org/10.1016/j.foreco.2016.10.057

Von Holle B, Neill C, Largay EF, Budreski KA, Ozimec B, Clark SA, Lee K (2013) Ecosystem legacy of the introduced N_2-fixing tree *Robinia pseudoacacia* in a coastal forest. Oecologia 172: 915–924. https://doi.org/10.1007/s00442-012-2543-1

Wagner V, Chytrý M, Jiménez-Alfaro B, Pergl J, Hennekens S, Biurrun I, Knollová I, Berg C, Vassilev K, Rodwell JS, Škvorc Ž, Jandt U, Ewald J, Jansen F, Tsiripidis I, Botta-Dukát Z, Casella L, Attorre F, Rašomavičius V, Ćušterevska R, Schaminée JHJ, Brunet J, Lenoir J, Svenning J, Kącki Z, Petrášová-Šibíková M, Šilc U, García-Mijangos I, Campos JA, Fernández-González F, Wohlgemuth T, Onyshchenko V, Pyšek P (2017) Alien plant invasions in European woodlands. Diversity and Distributions 23: 969–981. https://doi.org/10.1111/ddi.12592

Webb CO, Peart DR (2000) Habitat associations of trees and seedlings in a Bornean rain forest. Journal of Ecology 88: 464–478. https://doi.org/10.1046/j.1365-2745.2000.00462.x

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and Community Ecology. Annual Review of Ecology and Systematics 33: 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Wild J, Kaplan Z, Danihelka J, Petřík P, Chytrý M, Novotný P, Rohn M, Šulc V, Brůna J, Chobot K, Ekrt L, Holubová D, Knollová I, Kocián P, Štech M, Štěpánek J, Zouhar V (2019) Plant distribution data for the Czech Republic integrated in the Pladias database. Preslia 91: 1–24. https://doi.org/10.23855/preslia.2019.001

Wohlgemuth T, Gossner MM, Campagnaro T, Marchante H, van Loo M, Vacchiano G, Castro-Díez P, Dobrowolska D, Gazda A, Keren S, Keserű Z, Koprowski M, La Porta N, Marozas V, Nygaard PH, Podrázský V, Puchałka R, Reisman-Berman O, Straigytė L, Ylioja T, Pötzelsberger E, Silva JS (2022) Impact of non-native tree species in Europe on soil properties and biodiversity: A review. NeoBiota 78: 45–69. https://doi.org/10.3897/neobiota.78.87022

Woziwoda B, Kopeć D, Witkowski J (2014) The negative impact of intentionally introduced *Quercus rubra* L. on a forest community. Acta Societatis Botanicorum Poloniae 83: 39–49. https://doi.org/10.5586/asbp.2013.035

Woziwoda B, Dyderski MK, Jagodziński AM (2019) Effects of land use change and *Quercus rubra* introduction on *Vaccinium myrtillus* performance in *Pinus sylvestris* forests. Forest Ecology and Management 440: 1–11. https://doi.org/10.1016/j.foreco.2019.03.010

Woziwoda B, Dyderski MK, Jagodziński AM (2021) Forest land use discontinuity and northern red oak *Quercus rubra* introduction change biomass allocation and life strategy of lingonberry *Vaccinium vitis-idaea*. Forest Ecosystems 8: 1–9. https://doi.org/10.1186/s40663-021-00287-y

Yan P, Lu X, Li W, Zhang J, Li P, Li Y, Wang K, Ding S (2023) Seasonal Variations in Plant Species Diversity and Phylogenetic Diversity in Abandoned Farmland of China's Huang–Huai Plain. Diversity 15: e922. https://doi.org/10.3390/d15080922

Zasada M (2017) Raport końcowy z tematu badawczego "Ekologiczne, gospodarcze i urządzeniowe konsekwencje występowania wybranych gatunków drzew obcych w Polsce" realizowanego w latach 2013-2017 przez Samodzielną Pracownię Dendrometrii i Nauki o Produkcyjności Lasu na zlecenie Dyrekcji Generalnej Lasów Państwowych w Warszawie. SGGW, Warszawa.

Supplementary material 1

Supplementary information

Authors: Sebastian Bury, Marcin K. Dyderski

Data type: docx

Explanation note: **table S1.** The mean diameter in breast height (DBH) for trees with DBH<5cm, calculated. **table S2.** List of all woody species present in study plots and allometric models used for foliage biomass estimation (table S3). **table S3.** Allometric equations determining the biomass of particular tree species recorded on the study plots. **figure S1.** Distribution of the study plots (n = 160). **table S4.** General characteristics of the studied plots: stand age, total aboveground biomass, invasive tree species aboveground biomass. **figure S2.** Histogram showing the distribution of invasive species aboveground biomass [Mg ha-1] in plots with *P. serotina* (n = 64), and plots with *R. pseudoacacia* (n= 64). **table S5.** Functional traits used in the study and their min/max/mean values, standard error (SE), coefficient of variation (CV) and completness for numeric traits, and number of classes, frequency and completness for categorical traits. **table S6.** Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-poor sites in spring. **table S7.** Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-rich in spring. **table S8.** Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-poor sites in spring. **table S9.** Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-rich sites in spring. **table S10.** Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-poor sites in summer. **table S11.** Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-rich sites in summer. **table S12.** Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-poor sites in summer. **table S13.** Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-rich sites in summer. **table S14.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in spring. **table S15.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in spring. **table S16.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in spring. **table S17.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in spring. **table S18.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in summer. **table S19.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in summer. **table S20.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in summer. **table S21.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in summer.

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